Spatial pattern and community assembly: does the configuration of stream networks influence their community structure?

A thesis submitted for the Degree of

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by

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To
my
family

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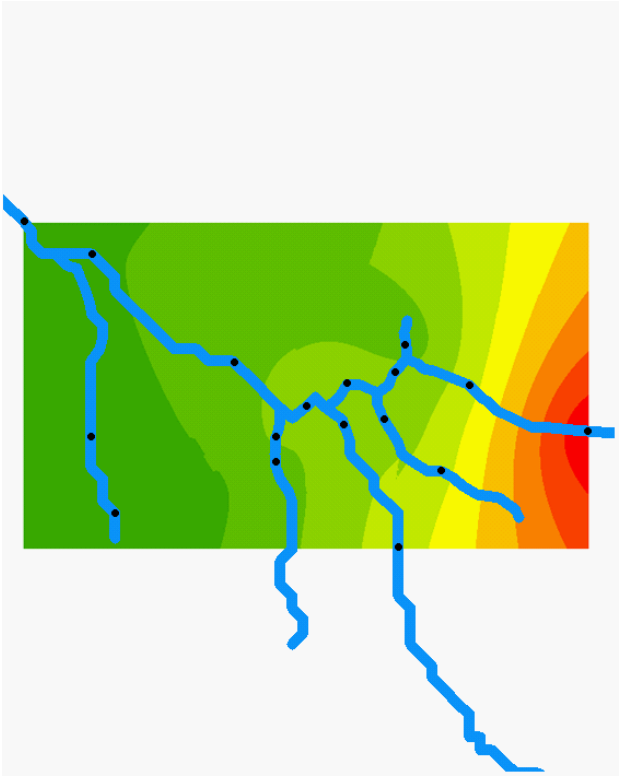
Abstract

Dendritic stream networks are inherently spatially and hierarchically structured, but the effects of this structure on stream communities are largely unknown. My aim was to investigate spatial patterns in stream networks using extensive spatial sampling of both adult and benthic macroinvertebrates in four stream networks on the West Coast of the South Island, New Zealand. Using spatial modelling and analyses, I answered questions about appropriate spatial measurements to capture ecological processes in stream networks, metacommunity processes at different scales in space and time, and how local and regional processes interact to structure metacommunities in stream networks.

Spatial eigenfunction analyses showed that distance measures that explained most variance in stream macroinvertebrate communities were stream distance and weighted stream distance measures. They performed better than Euclidean distance to measure spatial structure that is ecologically relevant to stream network communities. The spatial pattern of benthic stream macroinvertebrates was stable over time, whereas community composition changed significantly, as shown by space-time interactions modelled by MANOVA-like redundancy analysis. Thus, spatial processes structuring stream metacommunities remained constant, in agreement with neutral model predictions. Network-scale properties, particularly flood disturbances, influenced the relative importance of spatial and environmental variation in stream network metacommunities. Additionally, quantile regression indicated that three key variables, habitat size, isolation and local habitat conditions, jointly limited community structure in stream networks, providing empirical support for both island biogeography and metacommunity theories.

My study indicated that spatial structuring has an important influence on stream macroinvertebrate communities. The results contribute to broader ecological theory and understanding of community assembly by relating empirical results to theoretical predictions. In particular, they advance understanding of spatial processes in stream networks. The research also highlights a number of new methods, which were successfully applied to stream systems to elucidate complex spatial patterns.



“everything is related to everything else, but near things are more related than distant things”

-- Tobler’s 1st law of geography, Tobler 1970.

Preface

Investigating spatial patterns in ecology is important for testing specific hypotheses about controls and mechanisms of species distributions, such as dispersal and movement of individuals (Blanchet et al. 2008b, McIntire and Fajardo 2009). To investigate spatial patterns at multiple scales (Leibold et al. 2004, Resetarits 2005), stream networks offer a multi-scale, hierarchical organisation. The spatial branching pattern and stream flow direction have the potential to influence community structure, in addition to local habitat characteristics. Within the special spatial structure of networks, many stream invertebrates have multiple life history stages with various dispersal strategies. The adult and benthic life stages of aquatic invertebrates are likely to be influenced by different spatial processes, potentially resulting in complex combinations of spatial patterns and processes. Nevertheless, the importance of spatial arrangement of habitats in networks for dispersal and colonisation, and how it could subsequently influence community composition and dynamics, has had little attention (Kadmon and Allouche 2007, Economo and Keitt 2010). The hierarchical spatial arrangement of habitats in stream networks allows potential testing of many aspects of community ecology theory. Ecosystem size, distance between habitat patches and local habitat conditions are key predictors in many existing theories explaining species distribution and community assembly, such as the island biogeography theory (Kadmon and Allouche 2007), niche theory (Vandermeer 1972) and metacommunity theory (Leibold et al. 2004). Elements of these theories may be useful in predicting community structure, particularly those occupying networks, however they have primarily been developed as models, and empirical studies of real communities are rare.

While there has been a recent increase in theoretical metacommunity re-

search, few empirical studies of complex dendritic networks such as streams have been undertaken (but see Stewart-Koster et al. 2007, Brown and Swan 2010, Clarke et al. 2010). My overall aim in this thesis was to determine the role of metacommunity and spatial processes by investigating spatial distributions of both adult and larval benthic invertebrate communities in stream networks. I based hypotheses on established theoretical predictions to advance understanding of community assembly processes in stream network communities through empirical spatial sampling. Throughout this thesis, I assume that the spatial pattern in communities is ecologically meaningful, and that we can infer community processes, such as dispersal, from the resulting spatial arrangements (McIntire and Fajardo 2009). It is also assumed that more variance in community structure will be explained by spatial measures related to the actual processes structuring those communities. Using this landscape ecology approach to study communities in stream networks will reveal how the configuration of networks affects community structure and assembly. Such an explicitly spatial approach can add insight in stream networks, where movement of invertebrates is difficult to follow and experiments are unreasonable at large spatial scales.

I used spatial modelling approaches to test hypotheses regarding spatial patterns in community composition. These methods, concepts, ideas and approaches could be applied to many organisms or processes in dendritic networks, such as caves, hedgerows, riparian vegetation, and at a smaller scale, vegetation branches (Muneepeerakul et al. 2008a, Groot et al. 2009, Morrissey and De Kerckhove 2009), to advance ecological understanding and management of such systems. There is still much scope to investigate spatial patterns and processes in stream networks, such as how network configuration and spatial structure influence food web dynamics (McCann et al. 2005), patterns of species richness and species interactions (Lutscher

et al. 2007). However, due to the constraints of a PhD thesis, I necessarily restricted my approach, analyses and investigation to stream invertebrate metacommunity and community assembly processes in headwater stream networks. As such, I primarily used ordination approaches on species abundance data as measures of community composition to address important aspects of community spatial structure.

In the first chapter, I addressed which spatial distance measures are most appropriate for spatial stream invertebrate studies. Chapter two concerns spatial and temporal aspects of metacommunities and whether spatial patterns of stream invertebrates are constant over time. I then moved to a 'whole network scale' view, testing whether the relative importance of niche and neutral community structuring processes can be related to network scale variables such as disturbance regimes (Chapter three). Moving to smaller scale spatial processes, Chapter four addresses whether stream size and position in the network can help explain community variability in conjunction with local habitat variables. Finally, Chapter five summarises and explores my overall findings, putting them in the context of applications to management and ecological theory.

This thesis is structured as a series of stand alone papers intended for publication in international scientific journals. This means there is necessarily some repetition, particularly in methods sections, but this is an effective and efficient way to present the multiple facets of this work. All analyses and writing are primarily my own, with contributions of co-authors listed in individual chapter acknowledgements. Throughout the thesis, chapters are referenced by chapter number as they appear in this thesis. Figures and tables are numbered within each chapter, however the complete reference list is provided at the end to avoid replication. Appendices are also provided at the end for additional information toward some of the chapters.

“There is no single correct scale or level at which to describe a system”

-- Levin 1992

Chapter One

Spatial structuring of communities in stream networks: which distance measure is most useful?

Abstract

Streams are spatially structured systems characterised by dendritic geometry, but methods to describe spatial patterns in their communities have lagged behind those in terrestrial ecosystems. Spatial patterns should differ among stream organisms due to variable behavioural responses to directional flow and network configuration. Defining spatial patterns and their relevance to community structure can be achieved through determining different distance measurements between local, but interacting, communities in space. The most relevant distance measures will explain variance in community structure, and therefore various types of distance measure can be used to infer spatial processes. Furthermore, because community processes act at multiple spatial scales, the usefulness of particular distance metrics may depend on spatial scale. I investigated the usefulness of five different spatial distance measures in accounting for variation in macroinvertebrate community structure in four stream networks in New Zealand using eigenfunction analyses. First, I compared symmetrical Euclidean distance and stream distance using Moran's eigenvector maps. I then used asymmetric eigenvector maps to evaluate whether incorporating directional processes and weightings (e.g. by flow velocity) improved the variance explained in community spatial structure. Stream distance (mean explained variance, 15%), stream distance with directional upstream connectance (12%), and stream distance weighted by downstream water velocity (13%) were better measures because they captured more variance

in community spatial structure than Euclidean distance (9%). Furthermore, the distance measures which included hypothetical processes such as direction of movement and the influence of stream flow, explained smaller scale variation in community structure. Eigenfunction analyses provide a flexible range of useful methods to represent the spatial structuring of stream networks at multiple scales, enabling future use of a 'space as a surrogate' approach to investigate the behaviour and life cycle of organisms at scales which are difficult or impossible to measure directly.

Introduction

Communities can be structured by their physical environments and by biotic interactions, but the role of spatial location of interacting communities in determining local community composition generally needs more consideration (Thompson and Townsend 2006, Grant et al. 2007). Spatial autocorrelation, the degree of interdependence among observations in geographic space, is often seen as a nuisance, potentially causing statistical problems, but investigating the spatial structure of communities can also aid understanding of ecological systems (Lloyd et al. 2005, Thompson and Townsend 2006, Heino and Mykra 2008, McIntire and Fajardo 2009). Space can either be treated as a factor responsible for ecological structure, or as a confounding variable leading to bias when analysing other processes of interest (Dray et al. 2006). We demonstrate that taking the former approach can provide insight into the factors influencing the structure of communities that occupy spatially-structured environments such as streams.

Distribution patterns of ecological communities may be spatially autocorrelated due to community dependence on either spatially structured environmental factors, spatial community processes (e.g. dispersal and competition), or spatially dependent historical factors affecting community

structure (e.g. disturbance; Fortin and Dale 2005, McIntire and Fajardo 2009). Spatial relationships are likely to explain significant amounts of variance and should be introduced explicitly into statistical models (Dray et al. 2006). This is especially important in studies of streams due to their specific spatial structure (Wiens 2002, Fausch et al. 2002, Coté et al. 2009).

The linear nature of dendritic networks such as streams removes independence of communities within these systems, and unidirectional flow dictates that down-stream sites are likely to be influenced by upstream sites. The spatial non-independence resulting from this condition violates assumptions of standard statistical procedures and can lead to traditional analyses being too liberal (Rangel et al. 2006, Gardner and McGlynn 2009). Further complications, such as different levels of connectivity between habitats, not prevalent in lattice networks, also arise from the complex hierarchical branching patterns of dendritic networks (Benda et al. 2004, Grant et al. 2007, Morrissey and De Kerckhove 2009). Moreover, knowledge of the influences of spatial relationships on aquatic communities lags behind that of terrestrial spatial ecology (e.g. Urban 2004, Lowe et al. 2006, Grant et al. 2007, Labonne et al. 2008).

In many situations, direct measurement of spatial processes can be difficult or impossible (McIntire and Fajardo 2009). For example, dispersal is a key regulator of ecological processes, but it is difficult to measure empirically, and is often inferred from landscape pattern (Le Pichon et al. 2009). The spatial autocorrelation structure of communities can reveal information about the role of dispersal processes in bringing about observed patterns (Lloyd et al. 2005), and is being increasingly considered in ecological studies (Rangel et al. 2006). For example, McIntire and Fajardo (2009) promoted the use of 'space as a surrogate' for investigating or representing unmeasured processes. This 'space as a surrogate' approach requires ap-

propriate and precise spatial analysis techniques, which are only currently being developed. Flexible new techniques such as eigenfunction-based analysis (Dray et al. 2006, Blanchet et al. 2008b) offer good prospects for investigating spatial ecological patterns and processes, especially in the case of communities occupying dendritic networks.

The hierarchical scaling of spatial structure and flow connectance mean riverine ecology could be enhanced by the application of landscape ecology principles (Fausch et al. 2002, Benda et al. 2004). However, a landscape view is limited by a lack of understanding of network properties and their influences on the processes structuring communities within these networks (Benda et al. 2004, Grant et al. 2007, Coté et al. 2009). To measure effects of connectivity and spatial processes on communities in dendritic networks such as streams, appropriate distance measurements are needed. Distance measurements can be used to detect spatial structuring in communities, as the compositional similarity of communities should decrease with increased distance between the communities in space (e.g. Thompson and Townsend 2006). Thus, the variance in community composition explained by the distance measures indicates the level of spatial structuring between the local communities.

The most common measurement used to represent spatial structure in communities has been Euclidean (straight line) distance (e.g. Thompson and Townsend 2006, Heino and Mykra 2008). Euclidean distance, however, may misrepresent the connectivity and directionality of a dendritic network, and could be ecologically irrelevant for many biological processes (Peterson et al. 2007). Stream (hydrologic) distance is likely to be more appropriate in many aquatic landscapes (e.g. Le Pichon et al. 2009). Distance measurements used in stream studies also need to be complex enough to incorporate potential effects of directional flow (Morrissey and De Kerckhove 2009).

The appropriateness of the selected spatial measurements should also depend on the behaviour of organisms within communities. For example, whether they have passive drift, flight or swimming preferences would suggest whether directional spatial measurements would be more appropriate than, for example, straight line distances between communities (Figure 1). Spatial structuring can also be characterised by spatial scale (McIntire and Fajardo 2009). For example, large-scale spatial structuring may be driven by aspects of the landscape, so a distance metric such as Euclidean distance should explain large-scale variation. On the other hand, small-scale spatial structuring may be best represented by stream distance connections due to local interactions, such that movements of individuals and matter are more important at smaller scales.

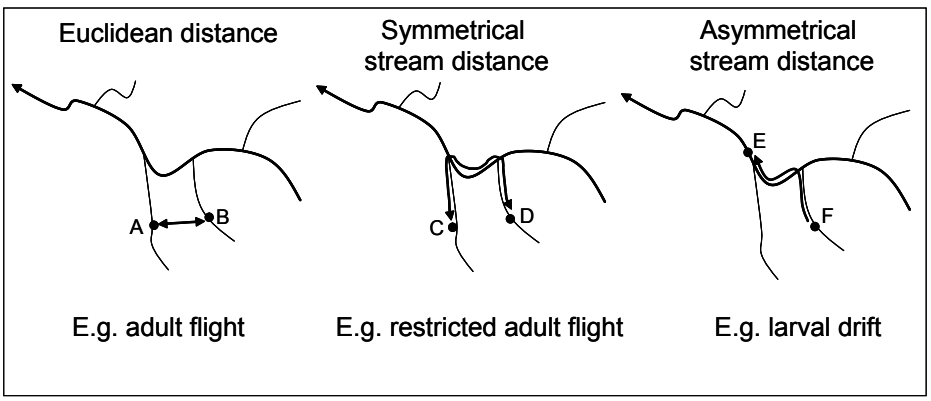


Figure 1. If individuals are restricted to movement in a stream, locations that are nearby in Euclidean space could be more isolated than those along network branches. For example, distance A to B may be effectively impossible to travel for many organisms, and although it is further in distance, C to D or F to E may be a more probable path for organism movement. A combination of these distance measurements might be useful for many stream invertebrates due to their complex life cycles involving larval stages restricted to the stream network and adults with the ability to fly and leave the stream corridor. Downstream stream distance (F-E) should be more appropriate where populations are connected predominantly by larval drift, or stream distance (C-D) more appropriate where adult flight dispersal is restricted to the stream channel. In contrast, Euclidean distance (A-B) may be the best measure if sites are connected by over-land dispersal.

The importance of spatial processes to stream ecology is being recognised, but statistical measures of spatial structure applicable to streams are relatively new and untested (Grant et al. 2007, Rodriguez-Iturbe et al. 2009). When using 'space as a surrogate' to represent spatial processes that are difficult to measure directly (McIntire and Fajardo 2009), we need measures that capture the real processes causing spatial structure in streams.

Necessary assumptions for ecological interpretation of this 'space as a surrogate' approach were that the more variance in community structure a distance measure explained, the more appropriate this measure was to explaining spatial processes in these communities. I also assumed that the processes captured in the distance measure (e.g. direction), would have ecological importance to the communities where this distance measure explained community variation.

I determined whether different spatial distance measures captured variation in community structure better than others in dendritic stream networks. More specifically, I tested whether Euclidean, stream or directional stream distances, explained the most variation in macroinvertebrate communities (species abundances) in four stream networks, on the West Coast of the South Island, New Zealand. I hypothesised that stream distances including directional distance would explain more variation in community structure than Euclidean distance, because the processes behind directional stream distance measures should be more ecologically relevant to stream macroinvertebrates. I also hypothesised that distance measurements should differ in importance depending on spatial scale as the mechanisms behind the spatial structuring should also act at different spatial scales.

Methods

Stream selection and sampling

Benthic macroinvertebrate communities of four head-water stream networks on the West Coast of the South Island, New Zealand were sampled, after the networks were mapped using a Trimble Recon hand held GPS (Figure 2). Each first order stream (defined as permanently flowing and > 30 cm wide with no incoming tributaries), had at least one sampling site, with longer first order streams having up to three. Sampling sites were located at least 50 m apart. Each stretch of second order stream between tributaries also had one to four sampling sites, depending on their length. This protocol resulted in the four stream networks having between 13 and 19 sampling sites allocated to capture as much spatial structure as possible (Figure 2). Sampling sites were 30 m stretches of stream, in which three replicate Surber samples were taken in riffle habitat (0.06 m^2, 250 μm mesh) to estimate macroinvertebrate community structure, and preserved in 70% ethanol in the field for later laboratory identification. Benthic macroinvertebrates were identified at 10 – 30 x magnification, to the best resolution available given the current taxonomy of larval stages (Winterbourn et al. 2006), and are hereafter referred to as species. Abundances were Hellinger-transformed before analysis to avoid the 'species abundance paradox' (Laliberté et al. 2009). In each 30 m reach, measurements of stream current were made to test whether velocity, which affects larval drift dispersal, could improve the effectiveness of distance measurements between communities. Mean velocity was determined at the water surface by timing a float over a known distance at base flow.

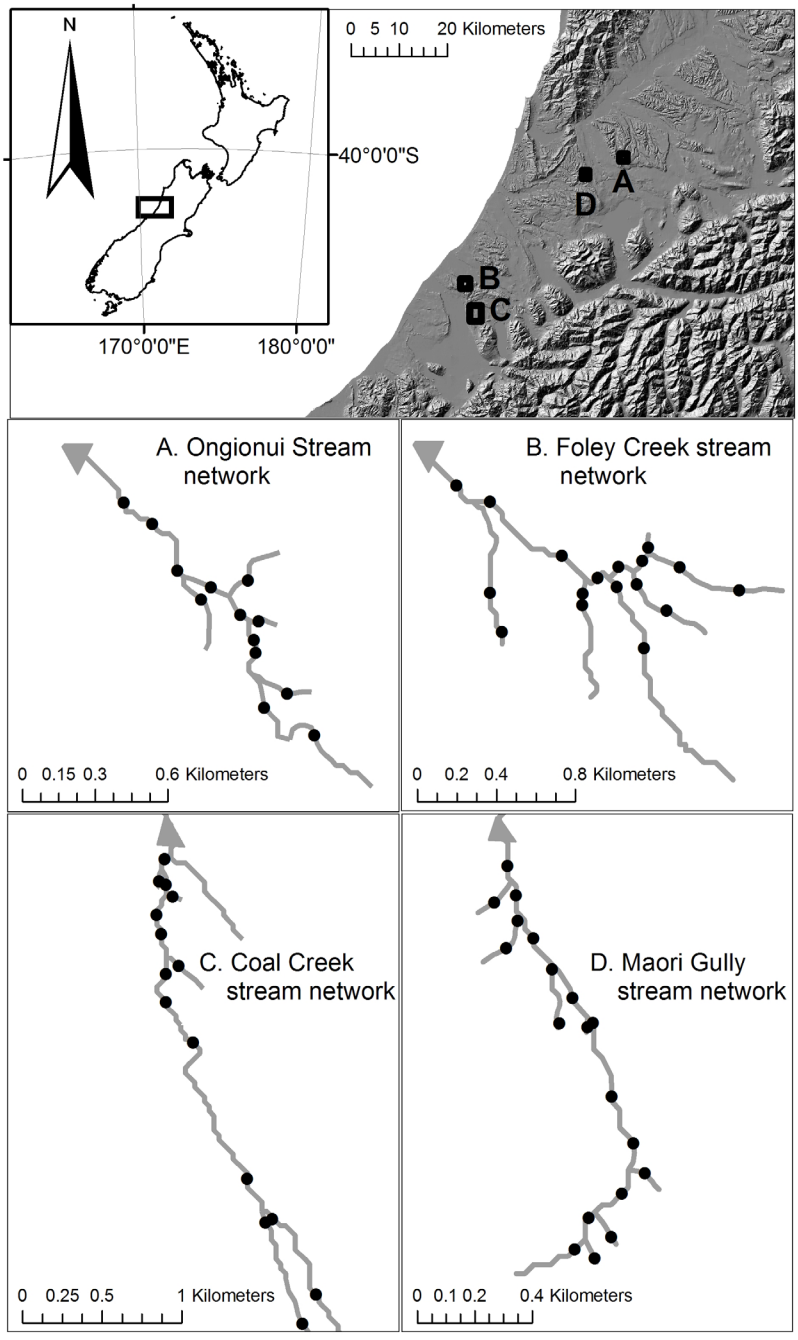


Figure 2. The four stream networks studied were located on the West Coast of the South Island of New Zealand. Arrows indicate the direction of stream flow and dots show locations of sampling sites. Shading in the top panel represents the topography of the area. Ongionui Stream had 13 sampling sites, Foley Creek 17, Coal Creek 15, and Maori Gully Stream 19.

Symmetrical distance measurements using Moran's eigenvector maps

Eigenfunction-based analyses include options for directional and weighted spatial representations with the potential to accurately represent processes in stream networks (Blanchet et al. 2008b). These methods are based on, and are comparable to, Moran's I statistics, which are the most commonly used statistics for autocorrelation analysis (Rangel et al. 2006). Eigenfunction analysis produces a set of eigenvectors which each represent an orthogonal spatial structure and can be used as explanatory variables in regression or canonical models (Dray et al. 2006). I used eigenfunction-based spatial filtering techniques to evaluate how well different distance measures accounted for variance in community structure (Rangel et al. 2006, Blanchet et al. 2008b). Moran's eigenvector maps (MEM) were used to test the importance of symmetric Euclidean and stream distances to structuring communities (Figure 1, Table 1). The symmetrical (i.e. the influence of site *i* on site *j* is equal to that of site *j* on site *i*; Dray et al. 2006) distance weighting measures I considered were Euclidean distance (EMEM) and stream distance (SMEM, Table 1). Euclidean distances between all sites were calculated within the R code for MEM from site coordinates, using packages 'vegan' (Oksanen et al. 2007) and 'PCNM' (Dray et al. 2006) in R (R Development Core Team 2007). Stream distances were calculated in ArcGIS using the Spatial Analyst toolbox and OD Cost Matrix tool (ArcMap 9.2) before they were used in the MEM R code.

Asymmetric distance measurements using binary connectivity matrices

To investigate whether directional distance measurements explained variance in macroinvertebrate community structure, I used asymmetric eigenvector maps (AEM), which are based on topology (connections and relationships between sites), because I hypothesised directional spatial processes would

influence the spatial structure of communities (Blanchet et al. 2008b). To represent down-stream processes (AEM1, table 1), we created 'binary connection matrices' with 0s and 1s representing the absence or presence of stream reaches linking each site to the top of all tributaries resulting in a measure of down-stream directional (e.g. flow) connectance between sites (Blanchet et al. 2008b). For upstream processes, the connections were based on whether or not the site was connected to the most downstream site (AEM2, Table 1; Blanchet et al. 2008b), thus representing potential up-stream movement.

To investigate more functional (directional and weighted) distance measures to explain spatial structure in communities, I multiplied the 'binary connection matrices' by weighting factors (Blanchet et al. 2008b). The weights I used were stream distance (AEM1 and AEM2, Table 1) and the combination of stream distance and flow velocity (AEM3, Table 1). The

Table 1. Five different spatial metrics were tested in four stream networks on the West Coast of the South Island of New Zealand. Eigenfunction -based spatial filtering techniques were used, allowing flexibility in weighting and directionality of spatial representation. I used two distance metrics using symmetrical distance based Moran's eigenvector maps (MEM), and three different asymmetric eigenvector maps (AEM) to represent different spatial structuring mechanisms and processes.

Distance measurement	Code	Description
Euclidean distance	EMEM	MEM on Euclidean distances between sites
Stream distance	SMEM	MEM on stream distances between sites
Direction – down-stream	AEM1	AEM connected from upstream site, weighted by stream distance
Direction – up-stream	AEM2	AEM connected from downstream site, weighted by stream distance
Direction and flow	AEM3	AEM from upstream site, weighted by stream distance and velocity

velocity weightings were calculated using the mean velocity of the upstream and downstream sites of each stream reach. Where the upstream site was on a tributary and the downstream site on the mainstem, the mean velocity of the sites on the tributary was used.

Comparing how distance measurements related to community structure

The adjusted coefficient of multiple determination (R^2_a), was used to compare the variance explained in the macroinvertebrate community structure by the different distance measurement models (Peres-Neto et al. 2006, Blanchet et al. 2008a). Each set of eigenvectors from each of the eigenfunction analyses for each distance measure, was subjected to forward selection ($\alpha < 0.1$) to detect eigenvectors explaining the most variance in community structure. The macroinvertebrate communities were then analysed as functions of the set of MEM and AEM eigenvectors by canonical redundancy analysis (RDA), a multivariate regression based analysis using the spatial vectors as predictors for the invertebrate communities. The RDA were followed by permutation tests produced by the 'anova.cca' function in the 'vegan' package (Oksanen et al. 2007) in the R statistical language (R Development Core Team 2007, Blanchet et al. 2008b).

Determining the scales of spatial relationships

To determine the scale of significant spatial structuring attributable to the various distance measures, each eigenvalue from MEM and AEM was used to represent a different scale of variation (Jombart et al. 2009). To compare the scales that each set of vectors for each distance measure represented, the eigenvalues associated with the forward selected eigenvectors were plotted for each distance measure and each stream network. Eigenvectors

were mapped onto their associated sites and interpolation (Kriging, Spatial Analyst toolbox; ArcMap 9.2) was used to visually display the spatial scales represented by the vectors.

Results

Macroinvertebrate communities

Macroinvertebrate communities in the four stream networks comprised predominantly Ephemeroptera, Plecoptera and Trichoptera taxa with the latter being most diverse (up to 32 Trichoptera species in a stream network). Ongionui Stream had a total of 77 species (15–47 per site), Foley Creek 63 (10–24 per site), Maori Gully Stream 81 (19–41 per site), and Coal Creek 67 (12–44 per site) (Appendix A).

Distance measure comparisons

Models using stream distance to explain variance in the macroinvertebrate communities performed consistently better than those using euclidean distance. However, the type of distance measure that accounted for the most variation in community structure depended on the individual stream network. Most variance explained in Foley Creek was associated with symmetric stream distance (SMEM). In contrast, Coal Creek community structure was best predicted by upstream distance (AEM2). Maori Gully and Ongionui Streams had most variance in community structure explained by downstream distance, weighted by water velocity (AEM3, Table 2). The next best distance measure explaining community structure in all streams, except Maori Gully Stream, was downstream distance (AEM1). For Maori Gully Stream it was symmetric (SMEM) stream distance.

Table 2. Differing amounts of variance in community composition were explained by the five spatial metrics in the four stream networks. This was determined using redundancy analysis (RDA) with forward selection (α <0.1 and 9999 permutations). The '# sig. vectors' indicates the number of vectors that were significant during forward selection, while 'variance' is how much variation in community composition this set of variables explained. The most significant distance metric for each stream is highlighted in bold with probability (P) values indicated. R^2_a is the correlation coefficient, adjusted for the number of variables in each model so that they can be compared robustly. Refer to Table 1 for distance measurement acronyms.

	# sig. vectors	Variance	P	R^2_a
Foley Creek				
EMEM	4	0.15	< 0.005	0.20
SMEM	**9**	**0.30**	**< 0.005**	**0.53**
AEM1	7	0.26	< 0.005	0.46
AEM2	4	0.17	< 0.005	0.28
AEM3	3	0.13	< 0.005	0.19
Coal Creek				
EMEM	3	0.098	0.005	0.19
SMEM	1	0.036	0.013	0.068
AEM1	3	0.11	< 0.005	0.24
AEM2	**5**	**0.15**	**0.005**	**0.28**
AEM3	2	0.073	0.01	0.15
Ongionui Stream				
EMEM	2	0.06	0.027	0.12
SMEM	3	0.11	< 0.005	0.26
AEM1	2	0.095	< 0.005	0.28
AEM2	2	0.076	0.005	0.19
AEM3	**5**	**0.15**	**0.01**	**0.37**
Maori Gully Stream				
EMEM	2	0.062	0.005	0.14
SMEM	5	0.14	< 0.005	0.35
AEM1	5	0.12	< 0.005	0.28
AEM2	3	0.093	< 0.005	0.23
AEM3	**7**	**0.16**	**0.005**	**0.40**

Scales of spatial structuring

The spatial scales of community structure the eigenvectors represented, can be determined by examining their respective eigenvalues; small scale spatial structuring in communities being indicated by smaller eigenvalues, and large scale spatial structuring by larger eigenvalues (Dray et al. 2006,

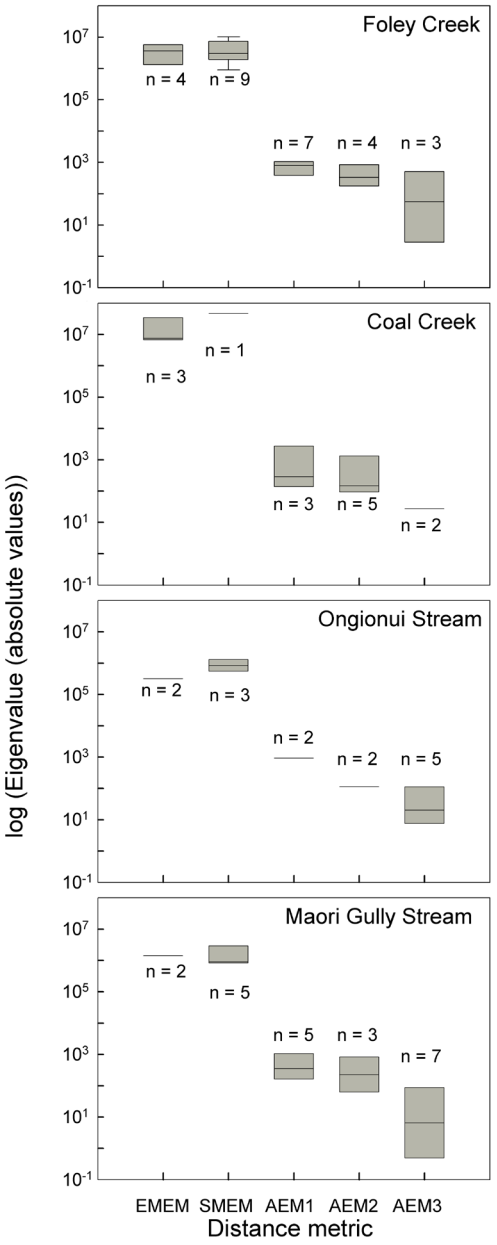


Figure 3. Variation in invertebrate community structure can be attributed to processes at various spatial scales by examining the eigenvalues associated with the vectors explaining significant variation. Larger eigenvalues (in absolute terms) indicate larger scale spatial autocorrelation, while smaller eigenvalues represent smaller scale spatial autocorrelation. The distance metrics compared here are Euclidean distance (EMEM), stream distance (SMEM) and asymmetric distances, distance downstream (AEM1), distance upstream (AEM2) and distance downstream weighted by flow velocity (AEM3) (see also Table 1). The y-axis shows the eigenvalues which represent different spatial scales with the boxes indicating median, 25th, 75th percentiles with 5th and 95th percentile error bars for these eigenvalues. The number of vectors included using forward selection ($\alpha < 0.1$) in each category is indicated by n.

Laliberté et al. 2009). The symmetrical stream distance (SMEM) vectors chosen by forward selection explained variance in community structure at the largest scale of all distance metrics, followed by Euclidean distance (EMEM) forward selected vectors (Figure 3). Smaller scale spatial patterns in communities were related to the variance explained in the community structure by asymmetric (directional) distance (AEM) vectors. The scale of variance explained decreased in spatial scale from downstream stream connectance, upstream stream connectance and finally, downstream stream connectance weighted by velocity explained the smallest scale variance components (Figure 3). Figure 4 provides an example of the

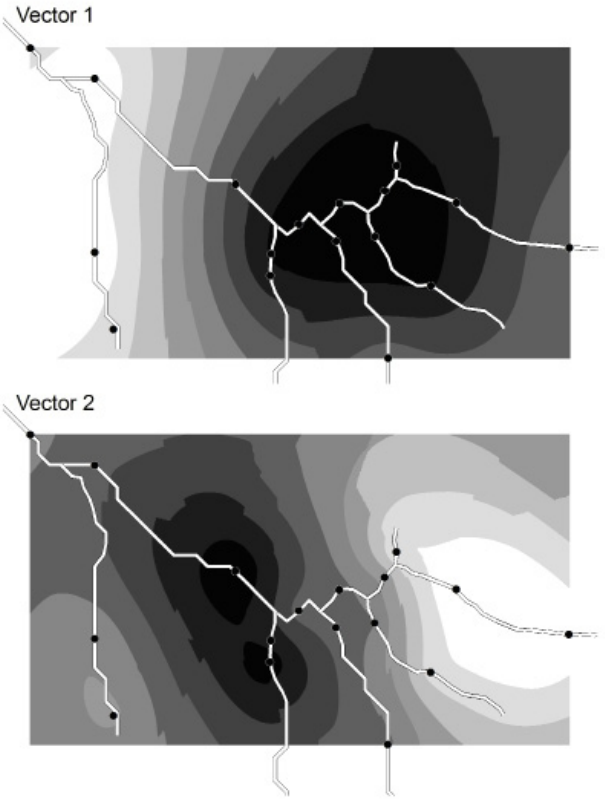


Figure 4. Maps showing spatial interpolation (Kriging, ArcGIS) between the eigenvectors giving a visual representation of the spatial scales they are associated with. Shown are examples of symmetric stream distance vectors (SMEM) one and two for Foley Creek. Streams drain to the top left hand corner, and black dots are the sampling sites. The shading represents the interpolated values of the eigenvectors attributed to each site.

visual representation of the scales of spatial variation associated with these vectors, where each MEM or AEM vector models a different scale of variation (Jombart et al. 2009). A more detailed table of all the forward selected vectors and associated eigenvalues along with significance levels is provided in Appendix B.

Discussion

Detecting spatial structure in communities using spatial distance measurements is important when investigating processes structuring communities. Using a 'space as a surrogate' approach (McIntire and Fajardo 2009), the detection of certain types of spatial structure in communities can be used to infer relevant community structuring processes such as type and extent of dispersal between local communities. This is particularly useful when directly measuring spatial processes is difficult or impractical, such as the large scale dispersal of small invertebrates. Euclidean distance has been the main metric used for detection of spatial pattern which may reflect ecological processes, however in stream networks, alternative distance metrics recognising dendritic structure and directional flow processes should be more ecologically relevant (Peterson et al. 2007). My results showed that this was indeed the case. Distance metrics that incorporated more spatial detail relevant to likely processes (e.g. downstream flow, dendritic network structure) explained more variance in macroinvertebrate community structure than traditional Euclidean distance measures. The ultimate choice of distance metrics will depend on the objectives of the research. For example, it needs to be recognised that although stream distance gave better correlations with macroinvertebrate community composition than Euclidean distance at the network scale in my study, at a multi-network scale, where

most catchments drain to the sea, stream distance could be meaningless measured through the sea, as most freshwater organisms cannot survive in saline conditions.

Potential processes responsible for spatial structuring

The exact cause of spatial structuring in macroinvertebrate communities considered in this study could not be absolutely determined. This was because my analyses did not distinguish between spatial dependence of communities (i.e. spatially structured environment) and actual spatial processes driving community structure (e.g. dispersal, movement). Because both types of cause are likely and do not function independently (Leibold and McPeek 2006, Lutscher et al. 2007), the results of applying different distance measurements will be useful for both partialling out spatial structuring and investigating specific mechanisms behind the spatial structuring. For example, even though the distance measure that explains the most variation in a community structure may reflect the influence of a spatially structured environment, it is still the most useful distance measure in that it represents the spatial structuring of processes (environmental or otherwise) in the stream network most accurately. Whether the patterns of community structure we observed are strictly due to dispersal of individuals dominated by passive drift, or whether the communities are simply structured by changes in the environment driven by directional flow, needs further study.

The importance of directional processes - dispersal or environmental change

One of the keys to the prediction and understanding of community structure is determining the mechanisms underlying observed community patterns (Levin 1992). Therefore, linking local demographic processes with spatial processes gives insight into controls on community dynamics. My results

suggested that the spatial patterns of stream macroinvertebrate communities were commonly better explained by stream distance, or stream distance with directional connectance. Although the stream distance measure that explained most variation in invertebrate community structure varied among networks, the predominance of the distance measure which incorporated aspects of downstream directional processes suggests that processes associated with directional stream flow are particularly important for stream macroinvertebrate communities. Directional dispersal and migration between populations occurs often in catchments and is thought to be a critical determinant of biodiversity patterns (Muneepeerakul et al. 2008a, Morrissey and De Kerckhove 2009). For example, Muneepeerakul et al. (2008a) found that adding dispersal directionality to models increased the probability of populations in networks going extinct.

Longitudinal gradients in abiotic and biotic conditions associated with downstream changes in discharge and channel morphology are common (Benda et al. 2004, Lowe et al. 2006). The River Continuum Concept (RCC; Vannote et al. 1980), the Serial Discontinuity Concept (SDC; Stanford and Ward 2001) and a more encompassing concept, the Hierarchical Patch Dynamics perspective (HPD; Poole 2002) all emphasised longitudinal spatial processes, and at least by inference, recognise the importance of longitudinal connectance and transfer of matter and energy through a stream network. The SDC and the HPD perspective also take into account how the position and influence of tributaries affects longitudinal patterns observed. However, there have been few empirical studies of these effects. My evaluation of eigenfunction-based spatial distance measures in explaining community structure indicates such measures will be particularly valuable for investigating longitudinal structure and effects of the arrangement of tributaries on communities in networks like streams, while also incorporating directional

processes.

The directionality of dispersal can play an important role in determining species distribution patterns as it creates bias in the dispersal of individuals (Lutscher et al. 2007, Muneepeerakul et al. 2008a). In stream ecosystems the presence of strongly unidirectional flow suggests that an asymmetric spatial model should have more relevance than a symmetric spatial model in predicting spatial community patterns. In two of the four stream networks we investigated, this was the case, with most variation explained by the downstream plus flow distance metric (AEM3). Moreover, in three streams, downstream distance explained the second most variance. This is comparable to the empirical results of Blanchet et al. (2008b) who found that the largest proportion of variation was explained by a directional AEM model rather than symmetrical distance models. Similarly, Lutscher et al. (2007) found that theoretical models of advection-diffusion dispersal depended on the velocity of stream flow. The fourth stream (Foley Creek) which did not have much variance explained by the downstream direction weighted distance, has a different branching pattern (Figure 2) which could indicate that the importance of down stream connection depends on the network's spatial arrangement.

Multiple processes can lead to more than one type of spatial structuring in ecological communities being detected. However, the presence of multiple causes could also mask the detection of other spatial processes. For example, if upstream flight compensates for downstream drift in aquatic invertebrate communities, we may see no directional spatial structuring. Upstream connectivity explained more variance in macroinvertebrate communities than downstream connectivity in Foley Creek, suggesting that upstream movement may be more important than downstream movement in structuring the communities of this stream network. This result implies

that understanding the flying adult behaviour and its influence on spatial community dynamics needs more emphasis, particularly in terms of how this movement relates to stream network spatial structure.

The influence of network topology on the relevance of spatial metrics

McIntire and Fajardo (2009) suggested that mechanisms and processes can be inferred from different spatial patterns. However, in streams this is complicated by the topology and branching patterns of each network. For example, the extent of branching and the branching angles, in addition to spatial configuration of habitats within a network, may affect fluxes of individuals and the importance of different types of dispersal processes in structuring stream communities (Lowe et al. 2006, Grant et al. 2007, Chaput-Bardy et al. 2009). Furthermore, the maintenance of genetic variation in populations is related to the interaction between spatial arrangement of populations and the extent of directional movement (Morrissey and De Kerckhove 2009). It is therefore possible that the branching patterns of these four streams could have some influence on the selection of different distance measurements. For example, the network in which the macroinvertebrate communities were most closely related to symmetric stream distances (Foley Creek), was the network with the longest tributaries and the least linear topology (Figure 2). Where streams are more branched than linear, a greater difference in importance of the various distance measurements would be expected, due to the greater contrast between distance measures between longer branches. The combination of dispersal directionality and network topology has important consequences for species abundance and distribution patterns (Muneepeerakul et al. 2008a). However, specific mechanisms underlying the effects of network shape and configuration on community structure are not well understood (Lowe et al. 2006), and

more investigation is needed of the effect the network structure has on communities in dendritic networks.

Distance measurements at various spatial scales

Spatial patterns in species distributions result from multiple co-existence mechanisms and processes occurring at different scales (Levin 1992, Leibold and McPeek 2006, Jombart et al. 2009). Problems relating to pattern and scale are central to ecology, but few empirical studies have applied multiscale approaches to dendritic networks (Lowe et al. 2006, Jombart et al. 2009). There is no single scale at which patterns and processes should be studied (Levin 1992), and a combination of various distance measurements is likely to be important due to the number of scales and processes involved in structuring communities. The importance of various distance measures should alter according to scale due to the mechanisms structuring communities also acting at a range of spatial scales. Indeed, the distance metrics that were intended to capture more mechanistic measures (e.g. directional, flow), accounted for smaller spatial scales of variation in community structure than the simpler Euclidean or symmetrical stream distances (Figure 4). The influence of spatially structured environmental variables on species distributions is mainly expected to occur on broad scales (Jombart et al. 2009, Rodriguez-Iturbe et al. 2009). Therefore in streams, larger scale spatial structure (i.e. the scales EMEM, SMEM best accounted for) may be largely attributable to environmental spatial structuring, whereas smaller scale spatial variation may be related to dispersal or species interaction processes. Our results also showed that the distance measure representing upstream processes, explained smaller scale variation in community composition than downstream connectance. This also makes sense as it should be more difficult for invertebrates to move against the

flow, so only smaller steps of movement would be possible in the upstream direction (this would imply the unimportance of adult flight movement).

Conclusions and suggestions for distance measurements in streams

To better understand spatial influences on stream community assembly, more complex distance measurements relevant to the spatial configuration and processes of stream ecosystems are necessary. Biological organisation does exist and it is important to understand the links between processes and patterns in ecological systems (McIntire and Fajardo 2009). Dendritic environments are not only restricted to stream systems, but similar methods and consideration of different distance measurements should also be relevant to mountain range, cave, edge habitat and branching plant ecosystems (e.g. Holl and Crone 2004, Groot et al. 2009, Morrissey and De Kerckhove 2009). The eigenfunction methods used in this study are flexible enough to incorporate various spatial representations, and can encompass the complications of dendritic network structures and directional processes. My results suggest the distance measurements I used will be ideal for testing multiple alternative hypotheses regarding community assembly processes operating in dendritic networks.

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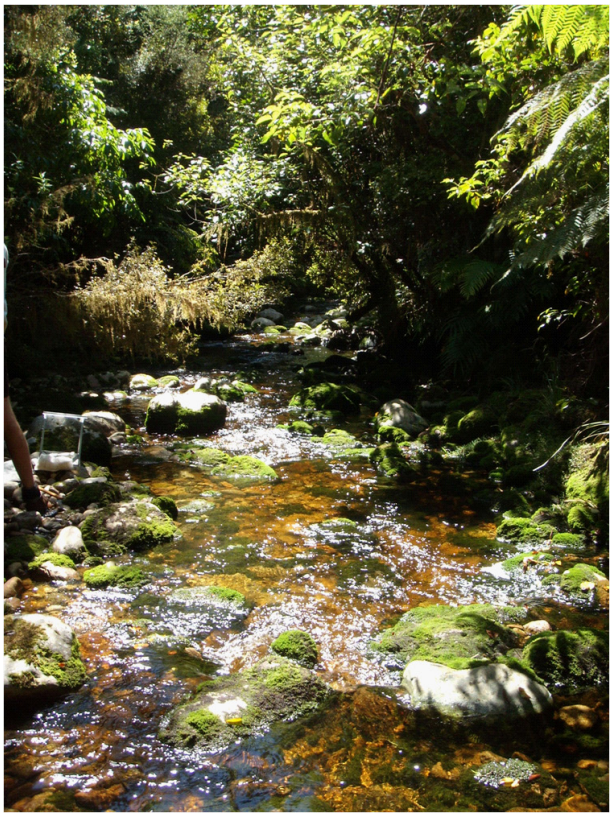

“All is flux: nothing is stationary”

-- Democritus

Chapter Two

Deterministic spatial structuring and invertebrate community change in stream networks

Abstract

Streams form hierarchical, dendritic networks, however little is known about how this spatial structure affects their communities. I investigated the potential for metacommunity processes in stream networks by measuring changes in macroinvertebrate community composition (species abundance) over time, and their distribution in space. Communities were sampled from every tributary, and every reach between tributaries, to determine effects of position in the network on community composition, in four headwater networks on the West Coast of the South Island, New Zealand. Using principal coordinates of neighbourhood matrices and a MANOVA-like redundancy analysis, I found that macroinvertebrate communities were significantly spatially structured and the species making up the communities changed significantly over time. The most important environmental variables (averaged over all models) explaining species turnover, were related to habitat size and isolation, disturbance and local habitat / resources. Nevertheless, a non-significant interaction between space and time indicated the spatial pattern of the communities remained the same, regardless of changes in species identity over time. This consistent spatial structuring could be the result of unchanging processes such as those arising from the universal nature of stream topology and hydrology acting both on dispersal- and habitat-related community processes. Moreover, the spatial patterns found indicated that stream communities could be driven by deterministic spatial processes in conjunction with stochasticity in the species making up the communities.

Introduction

Dispersal is a key factor linking community assembly theories and metacommunity hypotheses, and is important, not just because it adds stochasticity to the processes controlling species co-existence, but because it allows species compositional changes to track alterations in local environmental conditions (Leibold et al. 2004). Habitat size and the degree of isolation are important influences on dispersal processes and components of spatial structure, and are recognised explicitly in both island biogeography theory and meta-community models (e.g. Kadmon and Allouche 2007). Habitat size and isolation influence the risk of extinction and also the likelihood of recolonization via dispersal (Connor et al. 2000). The unique spatial arrangement of dendritic networks, with various levels of size and isolation, suggests that systems such as streams, planted windbreaks, riparian vegetation, roads and hedgerows could be ideal model systems for investigating complexities in metacommunity dynamics, such as relationships between dispersal processes and habitat size or location (Holl and Crone 2004, Muneepeerakul et al. 2008b, Groot et al. 2009).

Streams could be especially useful systems to explore these complex metacommunity dynamics because of their dendritic branching structures, juxtapositions of different sized habitats and varying connectance between habitat patches. Nevertheless, few studies have considered metacommunity-related aspects of stream systems (but see Thompson and Townsend 2006, Heino and Mykra 2008, Muneepeerakul et al. 2008b, Brown and Swan 2010). Treating streams as networks recognises the connected nature of their communities, and provides opportunities to test spatial influences on the relative importance of various community assembly mechanisms. Because community processes in dendritic networks can behave differently depending on the network structure (e.g. Fagan 2002, Labonne et al. 2008),

effective adaptation and application of traditional metacommunity principles are needed to advance understanding of community assembly processes in dendritic systems.

Although spatial arrangement and dispersal are major influences on metacommunity dynamics (Leibold et al. 2004), knowledge of change in communities over time is also crucial to understanding the dynamics of dendritic metacommunities (Rodriguez-Iturbe et al. 2009). Landscape structure is expected to affect population persistence within these spatially and temporally heterogeneous habitats, but because most environments are perpetually in a state of flux and do not have strict 'end points', community data obtained by ecologists often reflect a single point in time. Metacommunities change over time due to stochastic extinction and colonisation. That is, some suitable patches will not always be colonised, and potentially every patch will be at a different stage of colonisation at any given point in time, with combinations of species appropriate to the dynamic state of the patch. This is especially true of stream systems, where floods, low flows and drought can alter colonisation-extinction patterns (e.g. Pringle 1997, Death 2010). Although communities are expected to change over time, the underlying processes (i.e. colonisation, extinction and habitat associations) influencing these communities may not. It is therefore particularly intriguing whether spatial patterns of communities vary through time as this would indicate whether processes, as well as communities, fluctuate temporally (Laliberté et al. 2009).

Particular spatial arrangement of communities can arise from a spatially structured environment, from community processes such as dispersal or, more likely, from both (Thompson and Townsend 2006). However, when disentangling the relative importance of environmental- and dispersal-processes controlling community patterns, standard practice has been to

infer that dispersal processes are stochastically-driven, and related to neutral dynamics (e.g. Leibold and McPeek 2006, Thompson and Townsend 2006, Heino and Mykra 2008, Laliberté et al. 2009). On the other hand, deterministic processes are usually linked to the influences of local habitat conditions and niche assembly dynamics, where organisms are significantly influenced by their local habitat conditions (e.g. Leibold and McPeek 2006, Thompson and Townsend 2006, Heino and Mykra 2008, Laliberté et al. 2009). Complications in using this 'stochastic' versus 'deterministic' terminology arise because some habitat elements, such as disturbance, can also be stochastic, and dispersal can be deterministic, for example, when species select certain habitat types (e.g. Timm 1994, Peckarsky et al. 2000, Caudill 2005). Investigations are needed to disentangle the various interactions between habitat, dispersal, stochasticity and landscape structure, and their influences on community dynamics, assembly and persistence in a changing environment.

In this study I investigated spatial and temporal patterns of macroinvertebrate communities in stream networks. Specifically, I evaluated: 1) whether the spatial distribution patterns of communities changed over time, 2) whether community composition (species abundance and density) at each location changed over time, i.e., whether there was a significant space-time interaction, and 3) potential mechanisms for these changes. My results shed light on the metacommunity dynamics in networks, add to the general framework linking hydrology, geomorphology and ecology (Rodriguez-Iturbe et al. 2009), and advance understanding of the relative roles of stochastic and deterministic processes creating spatial pattern in communities.

Methods

Sampling design, site selection and stream network mapping

Four headwater stream networks on the West Coast of the South Island, New Zealand were mapped in the field using a Trimble Recon hand held GPS (Figure 1). Each first-order stream, defined as permanently flowing and > 30 cm wide with no incoming tributaries, had at least one sampling site, with longer first order streams having up to three. Sampling sites were located at least 50 m apart. Each section of second order stream between tributaries also had one to four sampling sites, depending on their length. This protocol resulted in the four stream networks having 13 to 16 sampling sites (Figure 1). Sampling sites were 30 m reaches of stream, and were sampled in January or February 2008, and again eight months later, in November or December 2008 (the end and beginning of the Austral summer, respectively).

Habitat variables

Sixteen local habitat variables were measured to help explain change in community composition over time and space (see Table 1). Disturbance scores were assigned at each of the 30 m sampling reaches using methods in Pfankuch (1975). These gave comparative measures of lower-bank and stream-bed disturbance and stability that have proven useful in characterising stream disturbance regimes (Death and Winterbourn 1995, Greenwood and McIntosh 2008). Resources known to be important for macroinvertebrate communities were also measured in each sampling reach, as were mean stream width and depth. Distances between sites (within each network) and to confluences were measured in ArcMap (v. 9.2) using the OD-Cost matrix tool in the spatial analyst toolbox.

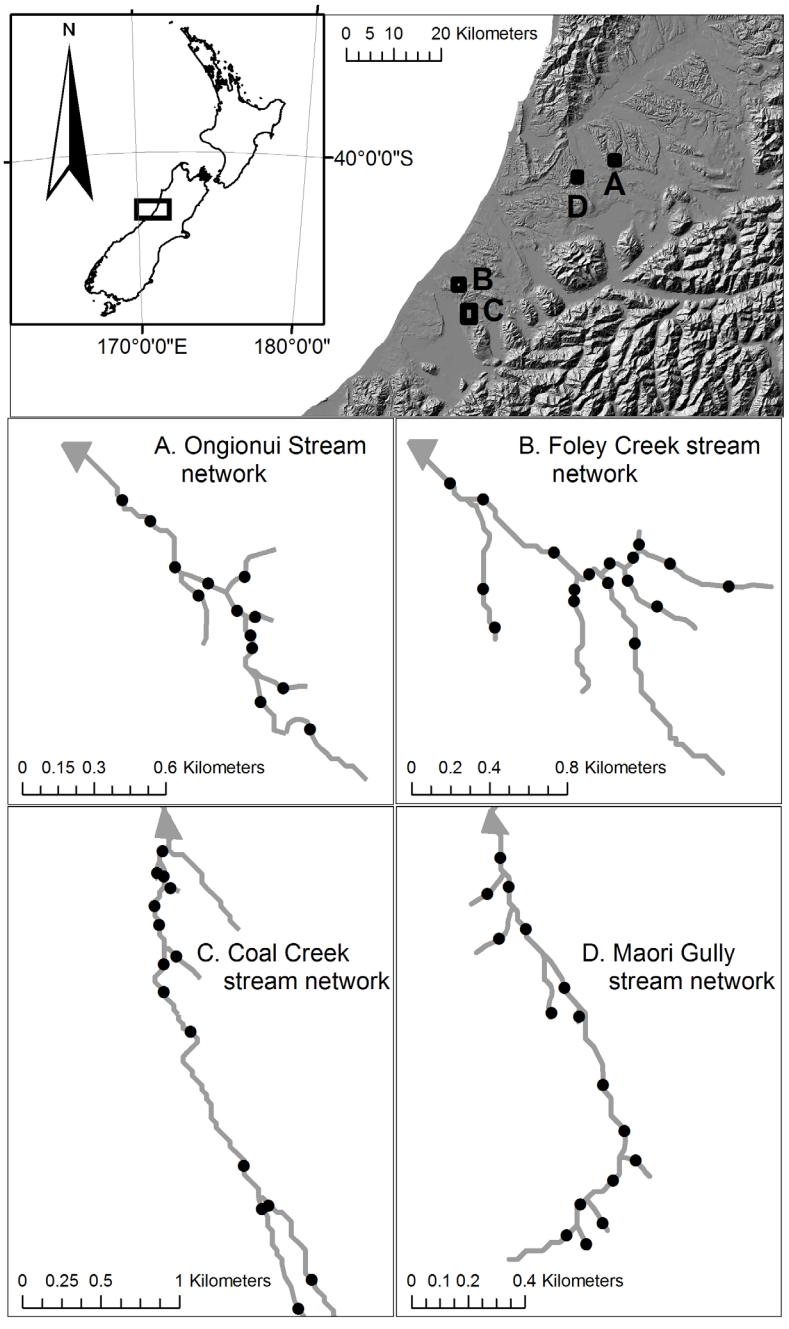

Figure 1. The four stream networks studied were located on the West Coast of the South Island, New Zealand. Shading in the top panel represents the topography of the area. Arrows indicate the direction of stream flow and dots show locations of sampling sites. Ongionui Stream has 13 sampling sites, Foley Creek 17, Coal Creek 15, and Maori Gully Stream 16.

Benthic macroinvertebrate communities

Three Surber samples (0.06 m^2; 250 μm mesh) were taken from random locations within riffles in each 30 m reach at each sampling date and preserved in 70% ethanol in the field. Benthic macroinvertebrates were sorted, counted and identified at 10–30 x magnification under a dissecting microscope. Immature aquatic insects were identified to genus or species using keys in Winterbourn et al. (2006). A consistent level of identification was maintained between sampling dates. Community composition was quantified as the abundance (density per m^2) of each species at each site.

Space-time interaction

The interaction between the effects of the spatial arrangement of communities and time on macroinvertebrate community composition was used to determine whether spatial patterns of macroinvertebrate communities in stream networks changed significantly over time. Spatial structure was quantified by creating principal coordinates of neighbour matrices (PCNM), thus creating vectors of spatial structure at multiple spatial scales, from a spatial distance matrix, to effectively capture complex spatial pattern in communities within stream networks (Dray et al. 2006, Laliberté et al. 2009). The PCNM procedure results in orthogonal spatial variables which can model spatial structure over a wide range of spatial scales and can be directly integrated into regression models, such as canonical redundancy analysis (RDA). The space-time interaction was tested for each stream network independently using a modified form of RDA, to provide an equivalent analysis to a multivariate analysis of variance (MANOVA, manovRDa; Laliberté et al. 2009). This manovRDa tested the relationship between a response matrix (species abundance data) and two crossed factors, the spatial PCNM matrix and time. To test for the significance of the main

Table 1. Local habitat variables measured at each site and used in the model comparisons using Akaike's Information Criterion (AICc). Spatial autocorrelation variables, stream, and stream distance from up-stream site were included as covariables in all models.

Variable	Units	Comment	Reference
Disturbance (lower)		Pfankuch disturbance score total for the lower stream banks	
Disturbance (bed)		Pfankuch disturbance score total for the stream bed	Pfankuch (1975)
Disturbance (total)		Total of upper, lower and bed Pfankuch disturbance scores	
Avg particle size	mm	Mean length of longest axis of 50 particles on stream bed	Gordon et al (1992)
pH		Spot measure using a hand held meter	
Avg depth	cm	Mean from three depths across the stream at four points along the 30 m stream reach	
Avg width	cm	Mean width of stream including dry gravels at four points along the 30 m stream reach	
Avg velocity	m/sec	Mean of three velocities taken over a 10 m section of stream	
SRP	µg/L	Soluble reactive phosphorus from water samples filtered in the field and frozen before analysing	
CPOM	g/0.06m^2	Ash free dry mass of coarse particulate organic matter (>1 mm) collected in a 25 x 25 cm Surber sampler	Hauer & Lamberti (1996)
FPOM	g/0.06m^2	Ash free dry mass of fine particulate organic matter (250 µm-1 mm) collected in a 25 x 25 cm Surber sampler	
Bryophyte	g/0.06m^2	Ash free dry mass of bryophytes collected in a 25 x 25 cm Surber sampler	
Canopy cover	%	Average percentage of canopy cover estimated from three digital photographs (ArcSinSqrt transformed)	

Table 1 (Continued)

Variable	Units	Comment	Reference
Distance up-stream to confluence	m	Distance along the stream network to the next confluence in the up-stream direction	
Distance down-stream to confluence	m	Distance along the stream network to the next confluence in the down-stream direction	
Distance to confluence	m	Distance along the stream network to the closest confluence	
Stream		Categorical coding for each stream network, Coal Creek, Maori Gully Stream, Foley Creek and Ongionui Stream	
Stream distance from up-stream site	m	Distance along the stream from each site to the most up-stream site in each respective network	

factors (space and time), Helmert contrasts (orthogonal dummy variables) were coded for in the RDA, while the space-time interaction was modelled using the spatial and temporal PCNM variables to overcome problems with lack of degrees of freedom (Laliberté et al. 2009). I treated both space and time as fixed factors and Hellinger-transformed macroinvertebrate community abundances to avoid the 'species abundance paradox' (Laliberté et al. 2009). The manovRDa procedure was carried out in the R program (R Development Core Team 2007) using the packages 'vegan' (Oksanen et al. 2007) and 'PCNM' (Dray et al. 2006).

Change in community composition related to habitat variables

For each network, non-metric multidimensional scaling (NMDS) using Bray-Curtis similarities was carried out on square root-transformed macroinvertebrate abundance data from each site, in PRIMER (Clarke and Gorley 2000). This resulted in a comparable measure of community composition within each network, with stress values < 0.2 indicating a good representation of community relationships between sites. Euclidean distances in NMDS ordination space between the same sites over the two sampling dates were calculated from axis 1 and 2 site scores in MatLab (The Maths Work Inc. 2008) to provide a measure of community change through time. To determine which environmental factors influenced the amount of change in macroinvertebrate communities, I used a model selection approach using Akaike's Information Criterion (AIC_c) in the program Spatial Analysis in Macroecology (SAM, Rangel et al. 2006), with Euclidean distance in the community NMDS space as the response variable. While my previous analyses were on the individual stream networks, this model selection method included all four networks as replicates. The response and predictor variables were all measured within and relative to the individual

stream networks. Because model selection analysis included all four stream networks, to account for spatial autocorrelation in the residuals, I included spatial variables in all models (Rangel et al. 2006). For large-scale spatial variation such as the differences *between* streams, a categorical dummy variable 'stream' (Coal, Maori, Foley, Ongionui) was included in all models. To account for autocorrelation *within* each stream, stream distance from the most upstream site (independent for each network) was included in all models. Results are displayed from the models that had change in AIC_c (ΔAIC_c) < 2 as these are statistically equivalent to the minimum AIC_c model (Rangel et al. 2006).

Results

Benthic macroinvertebrate communities

Ephemeroptera, Plecoptera and Trichoptera dominated communities in the four stream networks, with Trichoptera being the most diverse group. Species richness in each network ranged from 31 (Foley Creek, time one) to 58 (Maori Gully Stream, time two; Appendix A). Average densities ranged from 838 macroinvertebrates per m^2 in Foley Creek at time one (time two = 1450 m^{-2}) to 3993 m^{-2} in Coal Creek at time one (time two = 3086 m^{-2}). Maori Gully Stream had average densities of 3131 m^{-2} at time one and 3222 m^{-2} at time two, while Ongionui Stream had 3498 macroinvertebrates per m^2 at time one and 2462 m^{-2} at time two.

Space-time interaction

The lack of any significant space-time interactions indicated that the spatial patterns of community composition remained unchanged through time in stream networks (Table 2); the relative difference in communities, between

Table 2. Correlations resulting from a canonical redundancy analysis, functionally equivalent to a multivariate analysis of variance (MANOVA-like-RDA, manovRDa). The manovRDa was used to investigate the interaction of spatial structure in stream macroinvertebrate communities over time. Orthogonal principle coordinates of neighbourhood matrices (PCNM) vectors were used to code for space and time, to generate enough degrees of freedom to test the interaction of space and time. The R^2 is the variance explained by each variable in the manovRDa, while P is the probability value, with significant values ($\alpha < 0.05$) in bold.

	Space		Time		Interaction	
	R^2	*P*	R^2	*P*	R^2	*P*
Foley Creek	0.43	**0.008**	0.26	**0.001**	0.17	0.31
Coal Creek	0.66	**0.001**	0.07	**0.001**	0.13	0.55
Maori Gully Stream	0.65	**0.001**	0.085	**0.001**	0.14	0.53
Ongionui Stream	0.57	**0.001**	0.15	**0.002**	0.16	0.14

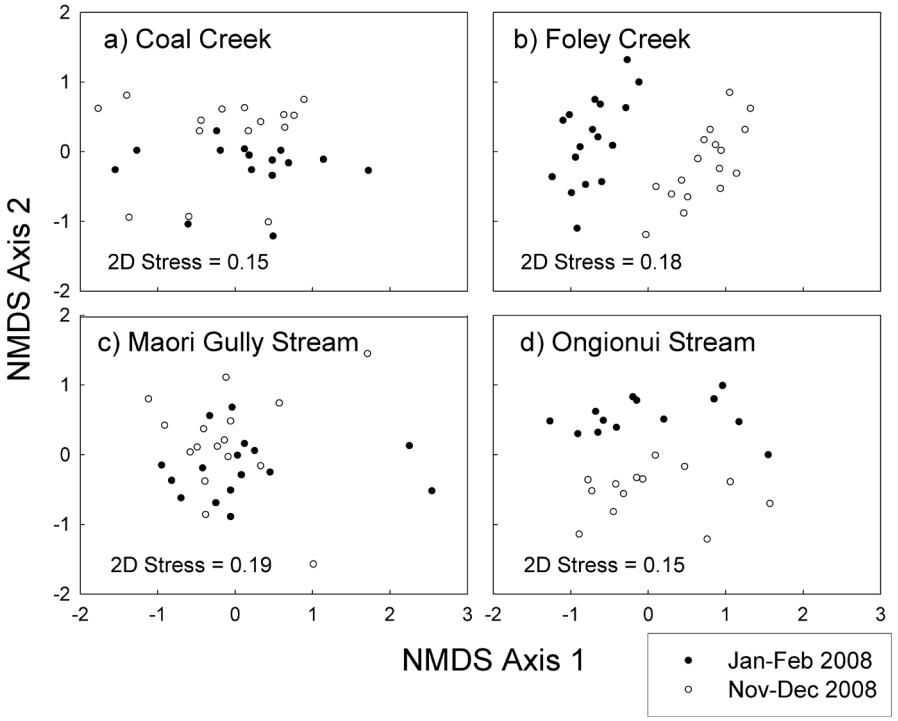

Figure 2. Non-metric multidimensional scaling (NMDS) plots of macroinvertebrate community composition in the four stream networks over two sampling occasions. Ordinations were based on square-root transformed abundance data using Bray-Curtis distances. Dots are individual site communities. Stress values were all < 0.2. Significance of changes between sampling times is reported in Table 2.

sites, within a network, remained similar. However, individual tests of both space and time effects on macroinvertebrate community composition were significant, indicating spatially structured communities, which varied significantly in species composition over time (Table 2). There were however, differing degrees of community turnover in species abundance and composition between the two sampling times depending on the network. For example, Foley Creek had the most obvious change, with communities shifting in composition mainly along axis one of the ordination space, while both Ongionui Stream and Coal Creek communities changed consistently along axis two of the ordination space. Change in the communities in Maori Gully Stream, although statistically significant, was more difficult to visualise in ordination space (Table 2; Figure 2).

Habitat variables related to change in community composition

The best model for change in species composition in communities, over all four networks, determined by Akaike's Information Criterion (AIC_c), explained 56% of the variance in the relationship between local habitat variables and the amount of change in the community composition between sampling dates. Five models with equal performance ($\Delta AIC_c < 2$) included combinations of eight of the 16 environmental variables (Table 3). The most important environmental variables (averaged over all models) explaining species turnover were related to habitat size and isolation, disturbance and local habitat / resources (Table 3). The changes in species and their abundances, were greater in reaches that were smaller, more disturbed, closer to confluences, with fewer bryophytes, and those that had higher levels of coarse and fine particulate organic matter and more neutral pH (Table 4).

Table 3. Models, which explained the most variance, as determined by the R^2 and Akaike's Information Criterion (AIC_c), in the amount of change in macroinvertebrate communities over two sampling times in four stream networks. The response variable was the Euclidean distance between sampling dates in the macroinvertebrate community non-metric multi dimensional scaling (NMDS) ordination space, and the predictors were environmental variables measured at each sampling site. All 16 environmental variables (see Table 1) were initially included in the models, but eight were selected for the optimal models, in addition to the spatial autocorrelation covariables. Stream network and distance from the headwater site (within each network) were included in the model to control for large- and small-scale spatial structure, respectively. AIC_c indicates the fit of each model taking the number of variables into account to avoid over fitting. A change in the AIC_c (ΔAIC_c) of < 2 indicates that these models were not significantly different in their ability to predict change in community composition.

Variables*	# variables	R^2	AIC_c	ΔAIC_c
1, 5, 7, 10, 14, 17, 18	7	0.555	86.101	0
1, 5, 7, 10, 13, 14, 17, 18	8	0.574	86.356	0.255
1, 5, 7, 10, 12, 14, 17, 18	8	0.567	87.325	1.223
1, 5, 7, 11, 13, 14, 17, 18	8	0.563	87.839	1.738
1, 7, 10, 12, 14, 17, 18	7	0.541	88.033	1.932

*1 = Disturbance (lower), 5 = pH, 7 = Average width, 10 = CPOM, 11 = FPOM, 12 = Bryophyte, 13 = Canopy cover, 14 = Distance up stream to confluence, 17 = Stream distance from headwaters, 18 = Stream.

Discussion

Although the identity of the species in stream network communities changed significantly over time, the significant spatial autocorrelation structure of the communities relative to each other within each network remained the same (i.e. there was no significant space-time interaction). This consistency in the spatial structure of communities suggests the processes underlying this spatial community compositional structure (regardless of whether they were community processes or spatially structured habitat associations) remained the same, and that species and abundance changes were common

Table 4. The importance (the number of times the variable is selected, averaged over all models) of each habitat variable in predicting the change in community composition between two sampling times, using the AIC_c model selection approach. The spatial variables, stream and stream distance from up-stream site had importance of one, as they were forced to be included in every model to control for spatial autocorrelation. The coefficients are shown to indicate the direction of the relationships.

Variable	Importance	Coefficient
Average width	0.85	-0.18
Distance up stream to confluence	0.84	<0.001
Lower bank disturbance	0.72	0.03
PH	0.71	0.22
CPOM	0.64	0.20
Canopy cover	0.51	0.41
Bryophyte	0.38	-0.32
FPOM	0.36	1.41
Stream distance from up-stream site	1.00	<0.001
Stream	1.00	-0.097

to all sites and in a common direction. These results reveal new information about the mechanisms behind the spatial structuring of communities which I discuss below.

Although the significant spatial autocorrelation structure could technically have been due to either spatial community processes or spatially structured habitat, if changes in local environmental and habitat conditions were responsible for species abundance changes, I would also have expected the relative spatial arrangement of communities to change (which did not happen). Some of the spatial structuring in my streams was related to habitat conditions (see Chapter 3), however the species composition at any particular niche can still not be predicted, as shown by the significant species turnover in my study. More specifically, the species making up a local community could be predicted relative to other communities in a network

by their spatial locations, but the community composition independent of other sites in the network could not be predicted.

Nevertheless, despite the species turnover, the spatial pattern of communities remained consistent, suggesting an element of deterministic structuring relating to the stream network spatial structure and dispersal processes such as dispersal limitation. These results suggest that the common use of the terms 'deterministic' interchangeably with 'niche'; and 'stochastic' interchangeably with 'dispersal processes' or 'significant spatial structuring', should be treated with more care. Spatial processes, including spatial dispersal processes, may not necessarily be 'stochastic' processes.

Dispersal can be deterministic (e.g. related to environmental conditions), potentially giving rise to the consistent spatial pattern I saw in my stream networks. For example, the spatial distribution of stream flow rate can influence the availability of resources and colonists at different locations in a network (e.g. the influence of down stream flow on drift dispersal; Lutscher et al. 2007, Rodriguez-Iturbe et al. 2009), and potentially lead to deterministically controlled stochastic dispersal processes. Moreover, deterministic and stochastic processes are not mutually exclusive (e.g. Thompson and Townsend 2006). For example, in my study, local habitat could represent a filter to select species from a species pool (e.g. Chase 2007), but the actual species present may depend on both stochastic processes and the spatial relationship to other communities. This could result in 'end point cycles' or 'alternative states' in community composition rather than simple deterministic community types (Chase 2007).

Consistent spatial structures indicate that the community-determining processes (whether environmental or dispersal-based or both) remained constant or reoccurred between the two sampling periods. This is in line with geomorphology, topography and catchment characteristics control-

ling stream network processes (e.g. Benda et al. 2004, Rodriguez-Iturbe et al. 2009). Geomorphology and topography control the branching patterns and riffle-run sequences in streams (Benda et al. 2004, Rodriguez-Iturbe et al. 2009). They also drive many of the processes structuring communities such as habitat heterogeneity (Benda et al. 2004, Kiffney et al. 2006) and dispersal both via flow (Lutscher et al. 2007) and over land between stream branches (Grant et al. 2007). Thus, creation of certain flow environments and connections between parts of the dendritic stream network due to constant or predictable geomorphology and hydrology could be responsible for the consistent macroinvertebrate spatial patterns I observed.

The dendritic topology of stream networks strongly structures local habitat conditions (Benda et al. 2004), which would in turn naturally influence species-habitat associations. It therefore makes sense that processes controlling macroinvertebrate communities, like the landscape processes structuring dendritic networks, are consistent over time. Similar ideas have been around for decades. For example, the river continuum concept (RCC; Vannote et al. 1980) suggested a consistent change in communities down-stream based on resource supply and resource spiralling. However, the RCC does not take into account branching patterns or dispersal processes potentially driven by network structure. Larval drift is an important dispersal process influenced by water velocity (Lutscher et al. 2007), and if the hydrological processes are consistent (e.g., they always flow to the same place due to the constant dendritic topology), then drift-dispersal relationships between sites would remain the same. Also, depending on the behaviour of winged adult aquatic insects, the amount and direction of adult flight relative to each location in a network could remain relatively constant, resulting in consistently spatially structured benthic communities.

What mechanisms result in greater community change?

Although the spatial structure of the macroinvertebrate communities remained the same over time, the species composition of the community changed. I wanted to determine whether any environmental variables could help explain this change, i.e. what habitat variables were correlated with greater species turnover. It is likely that a combination of factors were responsible for these changes, but most importantly, to induce change, processes of colonisation and extinction are needed (Leibold et al. 2004). Certain aspects of the habitat could affect the likelihood of the same or different species colonising, and the likelihood of extinction events, enabling recolonisation. Indeed, although simply a correlative response, I found that the environmental predictors most important in predicting how much communities changed over time, were associated with aspects of habitat size and isolation, lower bank disturbance, and resource availability, of which all could be factors influencing stochastic extinction and species pools available for recolonization (Kadmon and Allouche 2007, Cecala et al. 2009).

I discovered that the community composition of larger streams changed less over time, than in smaller streams. Although this has not been detected before in streams, it is not unexpected as the probability of stochastic extinctions decreases with habitat size (e.g. Connor et al. 2000, Holl and Crone 2004, Kadmon and Allouche 2007), thereby decreasing the chances of change in species composition. Habitat size in a stream network is also closely related to network structure, and the influence of confluence proximity on compositional change could be due to an interaction between network structure and organisms' dispersal (Convertino et al. 2009). The distance up-stream to a confluence likely reflects community isolation, with sites near confluences having greater potential to be connected, than those further from a junction. I found that the sites further from confluences up stream

(e.g. first-order streams), experienced the greatest species turnover. This could be attributed to isolation and thereby increased chances of stochastic extinction and species replacement. That is, increasing the likelihood of sites to be influenced by neutral or stochastic processes.

Further increases in the chance of stochastic extinctions were suggested by the importance of disturbance (lower Pfankuch), amount of bryophytes (often and indicator of disturbance; Duncan et al. 1999) and distance to an up-stream confluence, in predicting the amount of change in community composition over time. It is likely that disturbance promotes stochastic extinction, creating more opportunities for stochastic changes in species composition (Townsend et al. 1997b, Barnes et al. 2006), as indicated by my relationship between increased community turnover with increased levels of disturbance.

In addition to the disturbance, habitat size and locality related habitat variables influencing the amount of community change, resource supply or habitat suitability could also be important in predicting changes in community composition, as indicated by my correlative approach. I found an increase in canopy cover, CPOM, FPOM and a more neutral pH resulted in greater change in community over the two sampling occasions. Habitat harshness (in this case food shortage, less canopy cover, or acidity) can decrease the size of the potential coloniser pool (Chase 2007, Lepori and Malmqvist 2009), again, resulting in less chance for community composition to change. Even in these naturally acidic streams, pH might limit establishment of less acid-tolerant species. Moreover, FPOM and CPOM are important food resources for macroinvertebrates, while canopy cover could be indicative of either or both food resources and habitat suitability (Collier and Winterbourn 2000), thus affecting the size of the potential coloniser species pool.

Implications for stream ecology and metacommunity theory

In my study, covering aspects of communities in both space and time, I uncovered consistent spatial structuring in communities over time. This has important implications for current interpretations of spatial structure. Although my results do support neutral or stochastic processes controlling communities (Thompson and Townsend 2006, Laliberté et al. 2009), I also suggest that spatial structuring should not be entirely synonymous with stochastic processes. The resulting consistent spatial structuring could just as likely come from community structuring processes being determined by landscape configuration (e.g. landscape configuration determining the importance of neutral processes). Thus the changes observed in community composition, constrained within the physical network structure, likely result from both deterministic (but not necessarily local habitat / niche related) and stochastic processes. The space-induced stochasticity in community composition can potentially be related to deterministic dendritic network structure, a more complicated combination of neutral and deterministic processes than previously hypothesised. Despite the variety and complexity of dendritic systems, there appear to be common processes and explicit spatial aspects, such as the topography and hydrology, that play a fundamental role in structuring communities in stream networks. This should lead to a unified framework for dendritic ecological networks rather than treating each network completely individually (Benda et al. 2004, Mac Nally et al. 2006, Grant et al. 2007). Moreover, understanding how the network properties influence community composition will shed new light on the mechanisms that drive community assembly and the relative importance of dispersal limitation, stochasticity, deterministic and niche processes in assembling communities.

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“You cannot step twice into the same river for other wakes are continually flowing in”

--Anon

Chapter Three

Disturbance-mediated metacommunity gradient in stream networks

Abstract

Community structure is determined by a combination of regional spatial processes such as dispersal and local processes, such as environmental and biotic interactions. Where and why a combination, or just one of these community assembling processes are important, is poorly understood. I investigated the relative importance of spatial (e.g. dispersal) and environmental processes in determining metacommunity dynamics in stream networks. My aim was to detect whether network scale characteristics of streams influenced the relative importance of niche and neutral community structuring processes. Spatial sampling of stream macroinvertebrates and partial redundancy analyses revealed significant associations of macroinvertebrate communities with both spatial and environmental predictor variables. The relative importance of spatial or environmental community controls was unimodally related to flooding disturbance. Both recently stable and recently disturbed stream networks had more significant spatial structuring in their communities than intermediately disturbed stream networks. These results suggest that the metacommunity type depends on the length of time since a period of stable flow. Dispersal traits, community evenness and network topology were determined as mechanisms driving the disturbance-mediated metacommunity types. I have shown that the timing of disturbance can influence metacommunities and that these empirical metacommunities also tend to fit theoretical predictions including aspects involving dispersal limitation, metacommunity topology and community evenness. These findings indicate metacommunity models need to be dynamic to capture processes over both space and time.

Introduction

Niche (e.g. local habitat) and neutral (e.g. stochastic dispersal) processes are intrinsically linked and can be jointly responsible for structuring communities (Smith and Lundholm 2010). They are hypothesised to be differentially important depending on both the spatial scale (e.g. Chase 2003, Chave 2004, Fukami et al. 2005) and the species involved, so the balance between niche and neutral processes can have various influences on community and species dynamics (Bohonak and Jenkins 2003, Leibold and McPeek 2006, Thompson and Townsend 2006, Adler et al. 2007, Zhou and Zhang 2008). Investigating the relative importance of niche and neutral processes in structuring communities, and how both processes combine to determine observed community patterns, is important for understanding processes controlling species richness and abundances, which are key ecological issues. Furthermore, determining under what circumstances niche and neutral community structuring processes may be separately or jointly important in structuring communities, would be particularly useful for understanding community assembly and processes maintaining sustainable ecosystems.

The most widely accepted metacommunity theories, species sorting, mass effects, patch dynamics, and neutral models, have been related to and identified by partitioning various combinations of spatial and environmental controls on community structure (Leibold et al. 2004, Cottenie 2005, Peres-Neto and Legendre 2010) (Table 1). In reality, however, these metacommunity definitions form a continuum of relative importance between interacting local environmental and regional spatial processes (Cottenie 2005). The categories of these metacommunity types are useful, to simplify explanations and mechanisms, but realistically they are a gradient from one extreme (e.g. neutral) to another (e.g. niche) and communities are unlikely to

Table 1. The main metacommunity paradigms representing a gradient from predominantly spatially to predominantly environmentally structured communities (Leibold et al. 2004, Cottenie 2005). The paradigms can also be detected in combination with each other and are therefore not independent processes.

Metacommunity 'paradigm'	Description	Spatial-environmental importance and gradient
Species sorting (SS)	Patch quality and dispersal jointly affect local community composition	Inferred when communities are related to environmental structure independent of spatial structuring
Mass effects (ME)	Where immigration and emigration are primary drivers of local community dynamics (a.k.a. source-sink, rescue effects)	Spatial dynamics independent of the environment. When dispersal is high ME and SS show similar outcomes (high dispersal overrides SS)
Patch dynamics (PD)	Local habitats do not influence the species inhabiting them. Spatial dynamics are dominated by local extinction and colonisation	Spatial structure independent of environmental structure detected structuring communities
Neutral model (NM)	Assumes ecological equivalence and dispersal limited communities. Community dynamics based on probabilities of species loss and gain	Inferred when spatial structure independent of environmental structure detected. Cannot be distinguished from PD without further information on dispersal, competition, extinction or colonisation

Environmental associations important (niche models, E|S)

Spatial pattern important (neutral models, S|E)

fit simply one or other category for all species, dispersal abilities and spatial arrangements. Therefore the relative importance of different combinations of processes that result in non-random species distributions, form a gradient of metacommunity types, within which specific categories fit under certain circumstances, but can be difficult to disentangle.

Despite discussion of how differences in partitioning of community variation into spatially- and environmentally-induced components can represent different metacommunity models (e.g. Anderson and Gribble 1998, Peres-Neto et al. 2006, Smith and Lundholm 2010), less is known about why communities are structured in these ways. The factors responsible for this continuum in metacommunity models are unclear. In particular, what makes communities assemble in ways that include either or both neutral and niche processes; and what situations lead communities to be more or less spatially structured remains to be determined. Further investigation is needed of when, and to what degree, both niche differentiation and stochastic processes influence community structure, both together and separately (Leibold and McPeek 2006, Adler et al. 2007). Stream communities within spatially structured river networks offer good opportunities to investigate these issues.

Multi-scale systems such as stream networks are in effect metacommunities with movement of individuals (e.g. dispersal) and resources between local communities (Leibold et al. 2004, Brown and Swan 2010). Stream networks provide excellent opportunities for testing effects of dispersal on community assembly because they incorporate many levels of spatial interaction (Lowe et al. 2006, Thorp et al. 2006, Grant et al. 2007). They have a variety of arrangements of stream size and location of habitat in a dendritic network. Stream macroinvertebrate larvae disperse within the stream, but their adult stages which can fly, are not restricted to the stream

network, which results in different levels of local community interactions in a metacommunity context. While maintaining networks of interacting communities, at the larger scale, catchments are absolutely defined by their watersheds. It is therefore possible to have replicate (although not identical) catchments containing networks of macroinvertebrate metacommunities as a framework for examining whether network metacommunities are predisposed to certain balances of 'niche' and 'neutral' controls.

I investigated network-scale variables that could potentially drive stream macroinvertebrate metacommunity structure. The factors involved could be a combination of properties of networks (Grant et al. 2007), influences of confluences (Benda et al. 2004, Kiffney et al. 2006), disturbance regimes (Lepori and Malmqvist 2009), and differences between macroinvertebrate species traits, such as dispersal ability (Cottenie 2005, Thompson and Townsend 2006). All these factors potentially affect how stream macroinvertebrate species move within their environment, and their subsequent community dynamics. For example, disturbance of the network (e.g. by flooding), could drive the position of a metacommunity along a metacommunity gradient via influences on the importance of recolonization and redistribution of individuals. In addition, the stream network configuration could affect potential dispersal pathways, dispersal limitation and connections between local communities and therefore where a community fits in a metacommunity gradient.

Consideration of the effects of disturbance on ecological systems is increasingly important in the face of climate predictions for stronger, more frequent and unpredictable disturbances (Vitousek 1994, Milly et al. 2005). Stochastic disturbances that can effectively reset community assembly, can be dominant forces structuring many communities (Townsend et al. 1997b, Death 2010). Furthermore, due to the spatial hierarchy in stream networks,

disturbance in one branch segment may be translated through the network resulting in the increased risk of local extinction in these directed systems (Grant et al. 2007). Stream networks, therefore, represent ideal systems to test whether a metacommunity gradient can be driven by disturbance and whether the influence is also related to habitat spatial arrangement such as network topology.

Network topology and longitudinal connectivity of networks are probably crucial for many stream processes, but are often disregarded as factors structuring stream communities (Benda et al. 2004, Lowe et al. 2006, Clarke et al. 2008, Coté et al. 2009). Connections between landscape structure and metacommunity structure has been hypothesised and modelled theoretically (e.g. Starzomski and Srivastava 2007, Economo and Keitt 2008), and these relationships could primarily be driven by different extents of dispersal limitation associated with different levels of habitat connectedness (Cottenie 2005, Labonne et al. 2008). We might, therefore, expect differences in metacommunity processes to be affected by levels of connectedness between stream network components, because spatial arrangement of habitat affects dispersal, extinction and recolonization (Sanderson et al. 2005).

The overall aim of this study was to determine whether network-scale characteristics of streams such as rates of flood disturbance and topology, changed the relative importance of local (niche) and regional (neutral, dispersal) community-structuring processes. The relative importance of different metacommunity processes, such as dispersal and habitat associations, were hypothesised to change with disturbance regime (e.g. high flow events). I also hypothesised that mechanisms determining a metacommunity gradient could be inferred from dispersal traits of macroinvertebrates and community evenness.

Methods

Study networks

I used data sets from six stream networks from the South Island of New Zealand with multiple macroinvertebrate sampling sites (Figure 1). The networks consisted of first to third order streams and had eight or more sampling sites on each network with data on local environmental conditions and macroinvertebrate communities. Four stream networks on the West

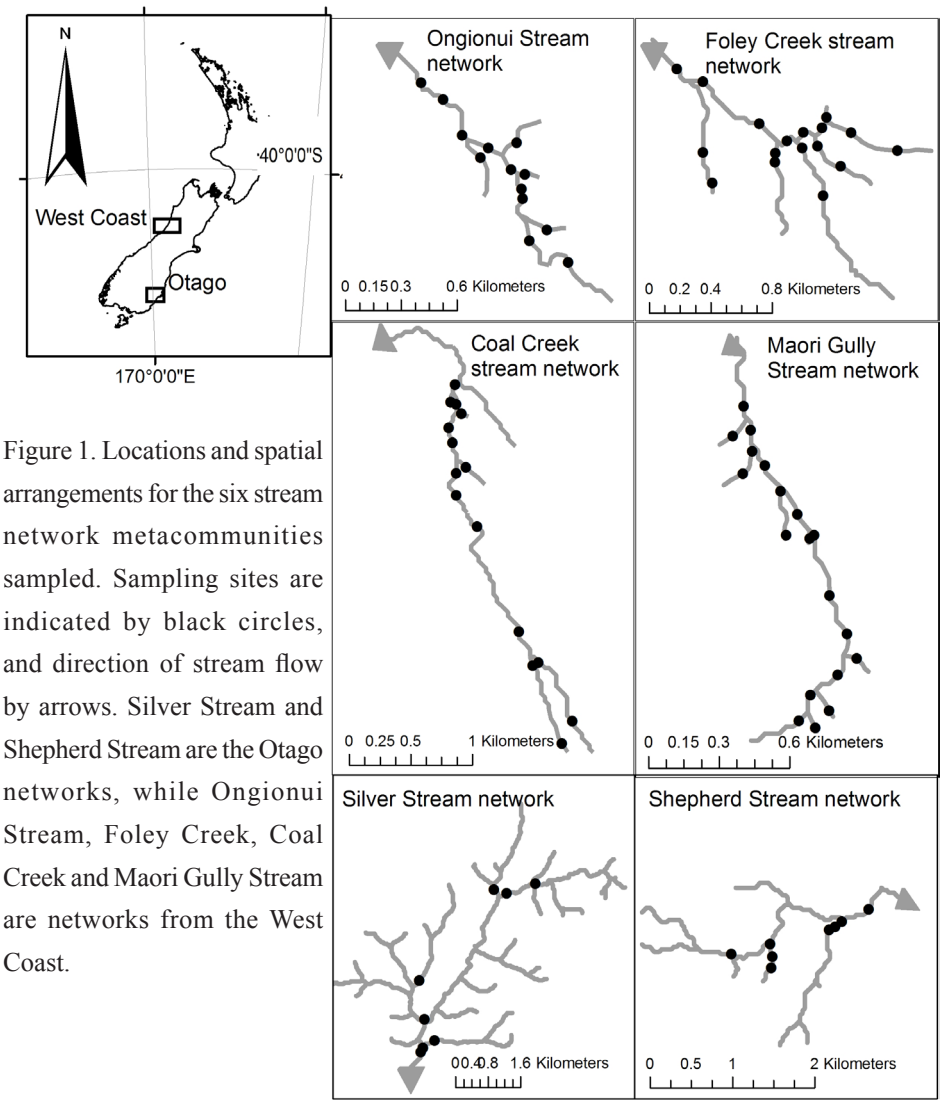

Figure 1. Locations and spatial arrangements for the six stream network metacommunities sampled. Sampling sites are indicated by black circles, and direction of stream flow by arrows. Silver Stream and Shepherd Stream are the Otago networks, while Ongionui Stream, Foley Creek, Coal Creek and Maori Gully Stream are networks from the West Coast.

Coast were sampled at two sampling periods (January-February 2008, November-December 2008), and two networks from Otago, sampled once (January-February 1990). The two West Coast sampling periods were treated as independent as the focus was on 'real time' hydrographs and community assembly, and the inclusion or exclusion of sampling time two data in the statistical analyses did not change any relationships except for decreasing statistical power.

Macroinvertebrate communities

The West Coast stream networks had sampling sites on every first order tributary and every second order reach between tributaries, and the Otago networks had similar, but a less regular spatial arrangement of sites (Figure 1). Benthic macroinvertebrates were sampled by taking two (Otago) or three (West Coast) Surber samples (25 x 25 cm, 250 μm mesh) from riffles in each of the 30 m sampling reaches in all networks (for more details on sampling in Otago networks see Townsend et al. 1997a). Samples were preserved in 70% ethanol in the field for later laboratory identification under a dissecting microscope using keys in Winterbourn et al. (2006). I used abundance data for taxa identified to a consistent level of resolution in each study and Hellinger-transformed them before analysis to avoid the 'species abundance paradox' (Peres-Neto and Legendre 2010).

Local habitat and spatial variables

Seven environmental predictors were used to represent habitat or niche components of the metacommunities (Table 2). To represent spatial structuring of macroinvertebrate communities in stream networks, spatial matrices were created using distance based symmetric Moran's eigenvector maps (MEMs) (Dray et al. 2006). Hydrologic distance measurements

between sites were calculated in ArcMap (v. 9.2) using the Network Analyst tool box and the OD-Cost matrix tool. Only vectors with significant Moran's I, representing significant spatial structuring were used ('all = FALSE' in the R code; Blanchet et al. 2008a), reducing the number of vectors (normally n-1 spatial variables are created) to maintain unsaturated models for further analysis.

Table 2. Seven environmental variables used in the global environmental models in the redundancy analysis (RDA), to relate macroinvertebrate communities to local stream habitat.

Variable	Units	Comment
pH or alkalinity		Spot measure using a hand held meter (West Coast) and chemical analysis (Otago)**
SRP or DRP	µg/L	Soluble Reactive Phosphorus from water samples filtered in the field and frozen before analysing*. Dissolved Reactive Phosphorus collected in the field for chemical analysis (Otago)**
CPOM	g	Ash free dry mass of coarse particulate organic matter (>1 mm) collected in a 25 x 25 cm Surber sampler
FPOM	g	Ash free dry mass of fine particulate organic matter (250 µm-1 mm) collected in a 25 x 25 cm Surber sampler[t]
Wood	%	Percentage of stream bed covered by wood over a 30 m reach (ArcSinSqrt transformed)
Leaves	%	Percentage of stream bed covered by leaves over a 30 m reach (ArcSinSqrt transformed)
Canopy cover	%	Average percentage of canopy cover estimated from three digital photographs (ArcSinSqrt transformed)

* Dev Niyogi pers. comm.

[t] Hauer & Lamberti (1996)

** See Townsend et al. (1997a) for more details

Spatial and environmental variance partitioning

I used variation partitioning using partial redundancy analysis (pRDA) to provide a standard and comparative method to assess the importance of environmental or spatial variation in structuring communities (Cottenie 2005, Dray et al. 2006, Peres-Neto and Legendre 2010). Sets of three matrices, an environmental matrix, a spatial matrix and a community matrix, were used to compare proportions of variation in the community explained by each predictor variable matrix using canonical pRDA. The amount of partitioned variance explained was represented by the adjusted R^2 (R^2_a), to control for any differences between stream networks for the number of sites, the number of explanatory variables and the probability of detecting effects (Peres-Neto et al. 2006).

I applied a forward selection procedure to obtain a subset of the spatial and environmental variables resulting in non-saturated global models (associations of communities with space (S) or environment (E) alone) before partitioning variance for space-habitat associations. For the forward selection procedure, I used two cut-off criteria, R^2_a of the global model and the alpha significance level (0.05) (Blanchet et al. 2008a). For each network, if either the global spatial model or global environmental model was significant, I proceeded with the partitioning approach to test the relative proportions of their independent effects on community structure. Analyses were carried out in R using packages 'vegan' and 'PCNM' (R Development Core Team 2007).

Network scale disturbance

A number of parameters for each reach of each stream network were entered into hydrological models using HEC-HMS (Hydrologic Engineering Centre-Hydrologic Modeling System) to produce accurate hydrographs for each

network (http://www.hec.usace.army.mil/software/hec-hms/index.html). Important parameters including rainfall data (http://cliflo.niwa.co.nz/), geology, land use and topography, were obtained from Geographical Information System (GIS) databases and field measurements (Appendix C). The output of these models gave hydrological measures which were relevant to the sampling times through determining flow patterns directly prior to sampling (raw hydrographs are available in Appendix E).

From the hydrological models, a number of disturbance measures could be calculated from the hydrographs. Disturbance relevant to stream communities has previously been measured by discharge, with variable results (Biggs et al. 1999, Duncan et al. 1999). Therefore, to encompass more cumulative effects of flooding (Matthaei et al. 1999), I used a measure of time (in days) since the last period of at least 7 days of base flow, determined from the HMS-HEC hydrological model. Relating disturbance to base flow incorporated non-catastrophic effects such as patchy bed movement during smaller spates as well as larger events (Matthaei et al. 1999). Base flow also represented a standard point of reference when comparing multiple streams from different regions (Biggs et al. 1999).

Network topology

To determine the importance of the connectivity of the stream and the associated communities, to the importance of dispersal processes, topological differences between networks were investigated. Drainage density, a measure of network dendricity, was calculated as the length of stream network per unit area of catchment (Benda et al. 2004) using ArcMap (v. 9.2).

Traits, community structure and evenness

Average trait scores of the macroinvertebrates in each network metacommunity were calculated as $\sum_i^n \frac{ty_i}{n}$ (Brown and Swan 2010). Where *t* is the binary (0 or 1) trait value, *y* is the proportion of the total species *i* (because abundances between networks were highly variable) and *n* is the number of species in the local community. The binary traits I used were flight dispersal (good or poor) and propensity to drift or move in water (good or poor) based on Poff et al. (2006) and expert knowledge (M.J.Winterbourn; Appendix D). To obtain a community measure for further investigating patterns of community structure, I used non-metric multi-dimensional scaling (NMDS) to obtain ordination scores for each network based on square root transformed average abundances and Bray-Curtis similarities in PRIMER (v. 5; Clarke and Gorley 2000). To further investigate which community characteristics could be influencing the proportion of community variance explained by spatial or environmental factors, a measure of evenness was calculated for each network metacommunity using the Simpson's diversity index defined as $D = 1 - \frac{\sum_{i=1}^{S} n_i(n_i - 1)}{N(N-1)}$, (PRIMER).

Mechanisms behind the relative importance of spatial and environmental processes

The ratio of variance explained by spatial structure independent of habitat variation (S|E) and habitat association independent of spatial structure (E|S) in each of the networks, was related to the network scale disturbance measure using polynomial regression (R Development Core Team 2007). Species traits and community structure were also related to the disturbance measure, and community evenness and network topology (drainage density) were related to the ratio of independent spatial structure (S|E) to independent habitat structure (E|S).

Results

Spatial and environmental variance partitioning

All networks, except Foley Creek, had more variance in macroinvertebrate community composition explained by the independent effects of environmental variables (E|S) than the independent effects of space (S|E; Table 3). Although more variance in community composition was explained by environmental structure, there were significant independent effects of space that simultaneously explained portions of the community variance. Four networks had significant independent effects of space (S|E, Coal Creek only marginally, Table 3). Variation jointly explained by environmental and spatial predictors which could not be statistically separated into independent effects of either space or environment (Peres-Neto and Legendre 2010), was relatively high. This was especially true in Foley Creek where joint variation exceeded both S|E and E|S portions of variation explained (Joint, Table 3). In the second sampling period, Ongionui Stream had no significant global models, and the ratio between S|E and E|S were not defined in either Foley Creek (F2) or Coal Creek (C2) so these were not used for further analyses.

Disturbance and metacommunity structure

The ratio of independent spatial variation to independent environmental variation (S|E:E|S) had a significant unimodal relationship with the number of days since a period of 7 days of base flow (i.e. time since stable flow period) ($r^2 = 0.86$, $p = 0.01$ (M2 included), $r^2 = 0.86$, $p = 0.05$ (M2 excluded), Figure 2). Thus, intermediately disturbed networks had a smaller proportion of community variation explained by independent spatial variation, than networks that were disturbed or stable. This corresponded to more spatial

Table 3. Spatial (S), environmental (E), independent spatial (S|E) and independent environmental (E|S) partitions of variation, and joint variation in macroinvertebrate community structure in stream networks compared using partial redundancy analysis (pRDA). R^2_a, the adjusted correlation coefficient, was used for comparisons between the networks (see methods text for details). Significant (alpha < 0.05) probability values (p) are highlighted in bold. 'Joint' variation is the component shared by spatial and environmental variation which cannot be statistically separated. SS = Species sorting, ME = Mass effects, NM = Neutral model, PD = Patch dynamics (from Cottenie 2005, and see Table 1).

	Number	S		E		S|E		E|S		Joint		
	of sites	R^2_a	p	R^2_a	p	R^2_a	p	R^2_a	p	R^2_a	Residual	Metacommunity type[t]
Coal Creek (C)	15	0.07	**0.03**	0.31	**0.01**	0.05	**0.05**	0.30	**0.01**	0.015	0.64	SS (+ ME[x])
Foley Creek (F)	17	0.25	**0.01**	0.20	**0.01**	0.10	**0.03**	0.05	0.13	0.15	0.69	NM/PD
Maori Gully Stream (M)	19	0.16	**0.01**	0.22	**0.01**	0.10	**0.01**	0.16	**0.01**	0.07	0.68	SS + ME
Ongionui Stream (O)	13	0.00	0.68	0.11	**0.02**	0.04	0.25	0.20	**0.04**	0.00	0.80	SS
Shepherd Stream (Sh)	8	0.06	0.16	0.18	**0.01**	0.04	0.26	0.16	0.06	0.03	0.78	Undetermined
Silver Stream (Si)	8	0.00	0.53	0.15	**0.03**	0.001	0.40	0.17	0.13	0.00	0.83	Undetermined
Maori Gully time 2 (M2)	16	0.09	**0.02**	0.17	**0.01**	0.06	**0.03**	0.15	**0.01**	0.03	0.77	SS + ME
Coal Creek time 2 (C2)*	15	0.03	0.31	0.10	**0.01**	0.00	0.48	0.06	0.07	0.04	0.91	Undetermined
Foley Creek time 2 (F2)*	17	0.12	**0.01**	0.19	**0.01**	0.00	0.84	0.05	0.09	0.14	0.84	Undetermined

*the ratio S|E:E|S is undefined (S|E = 0) therefore these are not included in Figure 2

[t]from Cottenie (2005)

[x]marginal S|E significance

structuring of macroinvertebrate communities in both disturbed and stable stream networks.

Macroinvertebrate dispersal traits, community structure and evenness

Total macroinvertebrate community structure, as represented by the NMDS Axis 1 scores, was significantly unimodally related to the disturbance measure with the exception of the Foley Creek community, which had markedly different community structure to other networks (F, Figure 3a). There was an overall negative relationship between community evenness

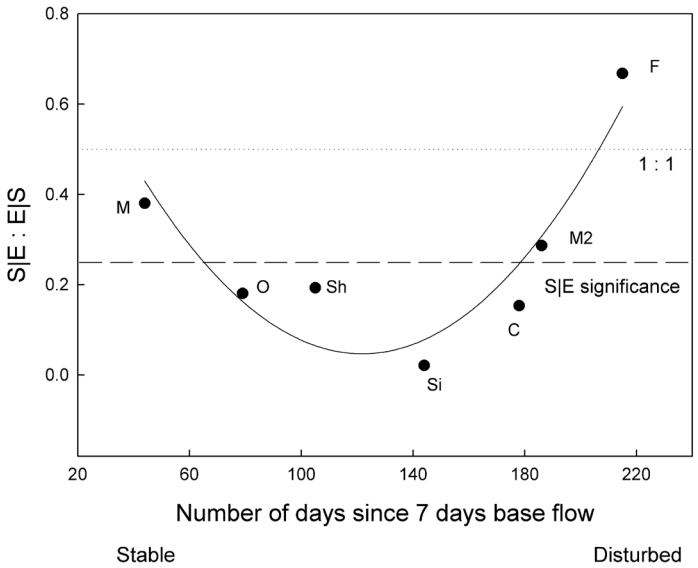

Figure 2. The ratio between variance in macroinvertebrate community composition in networks explained by spatial structure independent of environment (S|E) and environmental influences independent of spatial autocorrelation (E|S) was compared against the number of days since 7 days of base flow (i.e. time since period of stable flow). Base flow was determined from hydrological modelling (see methods) for the sampling time of each network. Network labels are defined in Table 3. The dotted line represents the 1:1 ratio where spatial and environmental community structuring processes are equally important. Above this line, variance in communities in networks was explained more by spatial structure, whereas below this line environmental influences explained more variance in community structure. The dashed line represents the line, above which independent spatial structure (S|E) was statistically significant.

(Simpson's diversity index) and the amount of independent spatial structure relative to independent environmental structure in the communities (Figure 3b). An obvious split was present over the evenness axis with the three most spatially-structured networks (M, M2, F, Table 3) having the most even or homogenous communities (Figure 3b).

Water dispersal ability of communities was negatively related to disturbance ($r^2 = 0.70$, $p = 0.04$ (including M2), $r^2 = 0.58$, $p = 0.13$ (excluding M2), disregarding Foley Creek), again with the exception of the most disturbed network, Foley Creek (F, Figure 4a). On the other hand, average flight dispersal ability of communities increased with increased disturbance, except

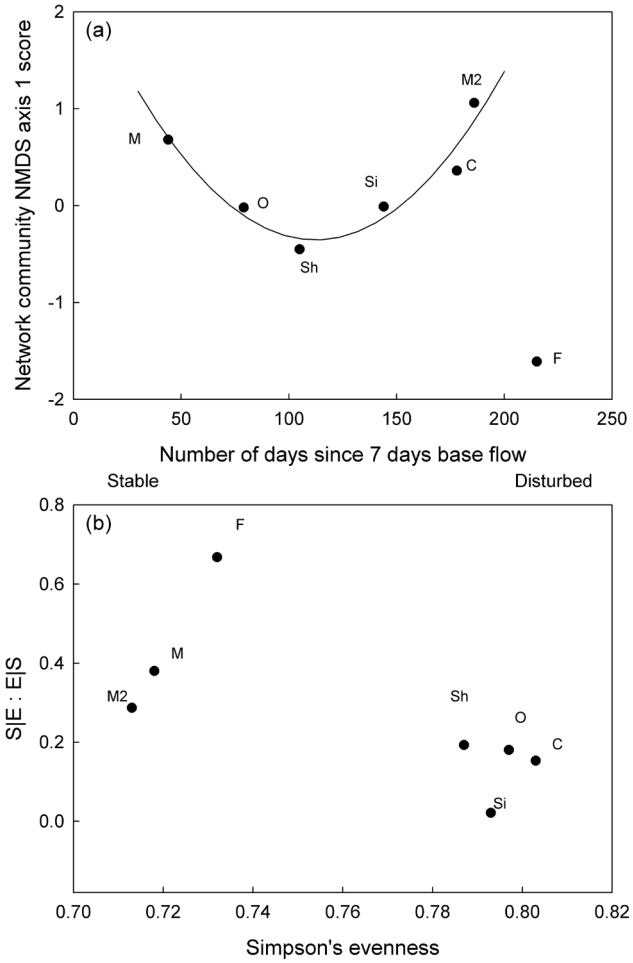

Figure 3. Community composition (a; Axis 1 NMDS) related to the number of days since a period of 7 days base flow and Simpson's evenness (b) compared to the ratio of spatially (S|E) and environmentally (E|S) related community variance.

the most stable site (M) and most disturbed site (F, Figure 4b). My measure of network topology, drainage density, had a positive linear relationship (r^2 = 0.49, p = 0.12 (without M2), r^2 = 0.41 p = 0.12 (including M2)) with the proportion of independent spatial variation to independent environmental variation (S|E:E|S) in stream macroinvertebrate communities (Figure 5).

Discussion

My goal was not only to investigate metacommunity and assembly types in stream networks, but also to determine whether network scale variables such as hydrological disturbance regimes, network topology, and species traits could be related to the importance of the various metacommunity

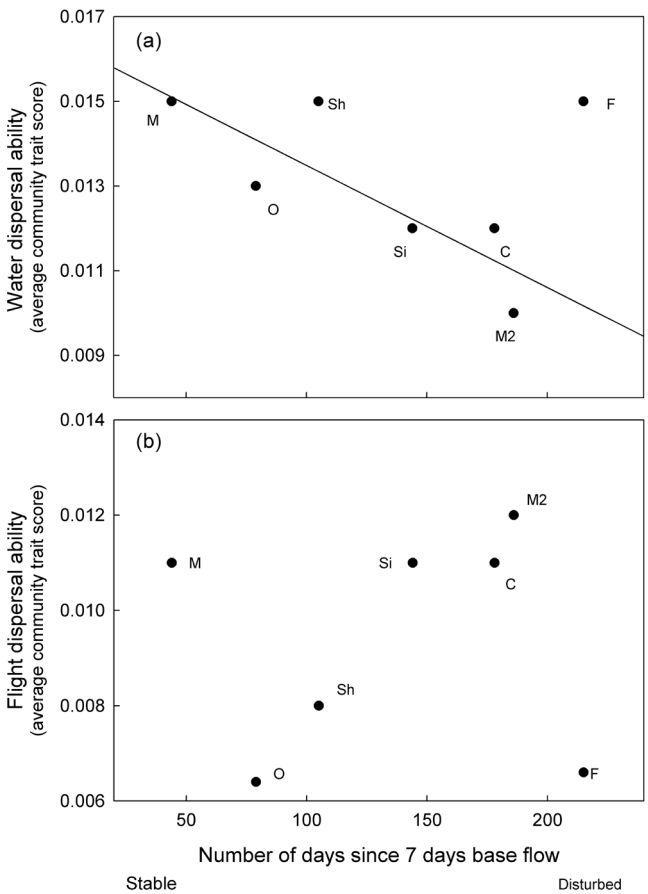

Figure 4. Average network community dispersal abilities for water dispersal (a, drift, swimming) and flight dispersal (b), related to the number of days since 7 days of base flow (significant regression line excludes F; traits assigned are found in Appendix D).

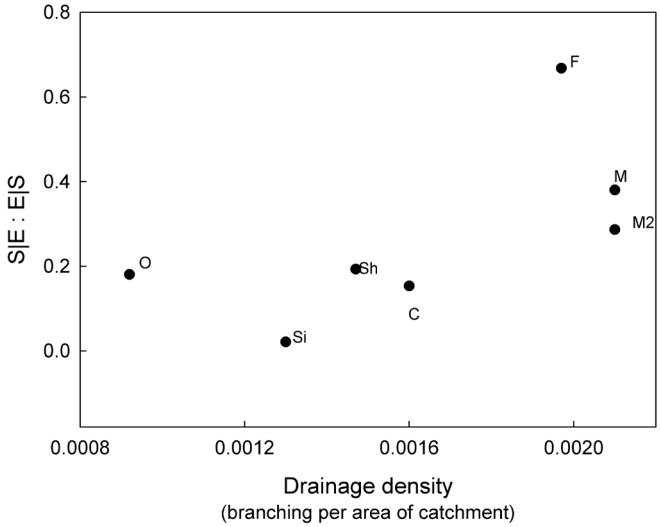

Figure 5. Ratios of community variance in stream macroinvertebrates explained by independent spatial (S|E) and environmental (E|S) processes related to drainage density or 'branchiness' of stream networks.

types present. Indeed, I found metacommunity types made up a gradient in the importance of assembly processes such as dispersal (spatial pattern) and habitat associations (environmentally structured community pattern). This gradient in metacommunity structure had a unimodal relationship with the network scale disturbance regime. Therefore, I found that benthic macroinvertebrate community structure in stream networks was determined by both local (habitat) and regional (dispersal) processes and a balance between these was mediated by the time since the stream network experienced a stable flow period. Studying streams at the whole network scale, where each network represents a metacommunity, meant that I could test hypotheses about how network scale variables affected metacommunity structure.

My findings indicated that a combination of metacommunity types were present at the network scale. Macroinvertebrate communities in three of the seven networks (M, M2, and C marginally) had significant components of variance in their communities explained by both independent effects of

space (S|E) and independent effects of local habitat (E|S). The combination of this relative importance of spatial and environmental community controls suggests the organisation of communities in these networks was best represented by species sorting (SS) and mass effects (ME) metacommunity models (Cottenie 2005). However, Foley Creek macroinvertebrate communities were only structured significantly by spatial processes independent of the environmental predictors, indicating neutral processes (NM) or patch-dynamics (PD) models were most appropriate. At the other end of the space-local habitat related metacommunity gradient, macroinvertebrate communities in Ongionui Stream (and marginally Coal Creek) were significantly structured only by environmental variables independent of spatial patterns, indicating potential species sorting (SS) dynamics (Table 3). Metacommunity types in the stream networks Sh, Si, C2 and F2 had significant global models, but showed no significant independent effects of space or local habitat on the macroinvertebrate communities and therefore they could not be clearly assigned metacommunity categories. There was typically a large shared component community variation where spatial structuring and environmental processes were confounded. In these situations either or both could be important but they cannot be statistically separated (Smith and Lundholm 2010). This was particularly prevalent in Foley Creek, where at both sampling times the joint environmental and spatial variations were 15 and 14% respectively, more than either of the independent spatial or environmental components (S|E or E|S) alone. This indicates a limitation of using only the significant separable variance components (Smith and Lundholm 2010), and therefore these joint influences need to be considered in conjunction with any variance partitioning results as they are likely to be common in ecological studies.

Network scale disturbance influences metacommunity structure

The relative influence of local and regional processes on community structure can be expected to vary over time (Mouquet et al. 2003), and indeed, in my study, the relationship between 'niche' and 'neutral' community controls changed unimodally with the amount of time since the stream network had a period of stable flow. The importance of spatial processes in structuring metacommunities varied depending on how recently disturbed the network was, or rather, how recently the stream had experienced a period of 'stable' flow. This indicates the importance of assembly time for communities to re-establish from the regional species pool (Mouquet et al. 2003). Observing the community during post disturbance recovery should increase the importance of stochastic processes in community assembly due to the importance of re-colonisation (Lepori and Malmqvist 2009). Stochastic processes of community assembly appeared to operate at both the stable and disturbed ends of the disturbance gradient I examined, and this pattern was also observed in Scandinavian macroinvertebrate stream communities in Lepori and Malmqvist (2009). The relative importance of spatial structuring and stochastic processes does not mean that local processes and interactions are not important in structuring these communities, as disturbance might obscure the signals from local conditions structuring these communities (Townsend et al. 1997b, Mouquet et al. 2003). The temporally dynamic, non-seasonal disturbances that I studied add novel support to the findings of Chase (2007) and Lepori and Malmqvist (2009), which were based on predictable or seasonal disturbance. My use of hydrological models provides a real-time representation of the hydrograph of the stream network given the catchment characteristics and the precipitation in the period leading up to the sampling time. This dynamic view adds insight (Lepori and Malmqvist

2009), as humans are changing disturbance regimes or creating disturbances which are not necessarily seasonally predictable (Milly et al. 2005).

To further investigate the mechanisms behind the community responses to disturbance, I examined the dispersal traits of the community (Brown and Swan 2010), and the 'branchiness' and topology of networks. Dispersal traits and network topology could influence community dispersal limitation, in turn affecting changes in communities over time and their recovery time after perturbations (Hendrickx et al. 2009, Brown and Swan 2010). I found that community composition had a unimodal pattern with assembly time, a similar relationship to the relative proportions of spatially and environmentally explained variation. Thus, these common unimodal responses indicated that certain types of communities were differentially influenced by local habitat or spatial processes. So what is it about the community and its phase in assembly time that would predispose it to being more structured by neutral or niche processes?

Communities seldom reach equilibrium state and disturbance can disrupt community assembly, continually setting processes back to an earlier stage (Townsend et al. 1997b, Mouquet et al. 2003). Flood disturbance can promote stochastic extinction and colonisation (Lepori and Malmqvist 2009) which would result in detection of spatial pattern. The prevalence of spatial structuring in my most recently disturbed networks could be attributed to the subsequent importance of dispersal and recolonization in structuring these communities as populations recover from disturbance through immigration and redistribution from refugia (Chase 2007, Starzomski and Srivastava 2007, Lepori and Malmqvist 2009). A short time after (re-) assembly has started (i.e. a long time since a period of base flow in my study), we would expect increased spatial structure as early colonisers, good dispersers and flood resilient species should make up these communities

(Lepori and Malmqvist 2009). I found that macroinvertebrate communities with a high proportion of good flight dispersers generally increased with increased disturbance, but not in the most stable (Maori Gully Stream) or the most disturbed (Foley Creek) networks. For the most disturbed network (Foley Creek), this may be due to severe or recent disturbance overriding dispersal traits (Lepori and Malmqvist 2009), and the most stable (Maori Gully Stream) potentially due to the importance of species interactions. On the other hand, disturbance has a patchy influence throughout the network (Matthaei et al. 1999), so macroinvertebrates may be redistributing within networks by different means. Species with high propensity and ability to drift and / or swim, generally decreased in proportion with increased disturbance. This could potentially be a response to catastrophic drift with more mobile species also more vulnerable and likely to decrease in abundance with increased disturbance.

The most even communities were also the most spatially structured. However, these occurred at both ends of the disturbance gradient. In recently disturbed networks, communities should be in an early stage of assembly and most species would be rare leading to an unsaturated community as only a subset of the regional pool would have had the opportunity to colonise (Hubbell 2003, Mouquet et al. 2003). Alternatively, a flooding disturbance event could reduce abundance, leaving only the common species, resulting in an even community. This matches the pattern observed in my most disturbed network, Foley Creek, which had high evenness/homogeneity.

I predicted more stable networks would have more advanced community assembly, leading to local habitat conditions driving community structure (Thomson et al. 2002). I found the converse, with increasing importance of spatial structuring in more 'stable' networks. When the environment is stable, communities may be assembled at random from the species pool

if the majority of species have the ability to exist under those conditions (Chase 2007, Lepori and Malmqvist 2009). In a stable scenario with replacement of individuals by stochastic neutral processes, common species should dominate due to their higher probability of colonising, resulting in relatively even communities (Hubbell 2003). Indeed, the communities I measured in my most stable network, Maori Gully Stream (M) were the most even. The importance of stochastic processes in the assembly of these communities are further indicated by the presence of high flight and water dispersal abilities in Maori Gully Stream (M) communities, and the additional dispersal limitation likely caused by its high drainage density. Note, however, that environmental factors are still jointly important at this end of the disturbance scale so a purely spatial/neutral explanation is not required and the spatial structure at the stable end of the gradient, although significant, is less than that driven by high disturbance.

The shape of network branching is expected to have strong effects on metapopulation processes, by affecting the movement of organisms (Fagan 2002, Starzomski and Srivastava 2007, Grant et al. 2009, Hughes et al. 2009). Therefore the structure of the stream network should affect connectivity and dispersal limitation, which in turn, would affect recolonization and community resilience after disturbance (Fagan 2002, Starzomski and Srivastava 2007, Labonne et al. 2008, Chaput-Bardy et al. 2009, Hughes et al. 2009). Neutral patterns (represented in this study by spatial structuring) should reflect geographic structure due to its effects on connectivity, speciation and metacommunity size (Economo and Keitt 2008). With increased drainage density (branches per unit area of catchment), my measure of network topology, I also detected an increase in the importance of the spatial fraction of variance in macroinvertebrate communities. Thus, increased dispersal limitation due to branchiness of a dendritic network was indicated by

the importance of neutral processes in structuring stream macroinvertebrate communities in the networks with higher drainage densities (F, M, M2).

Conclusions

Stream flow regime is one of the most influential physical features of lotic systems (Konrad et al. 2008) and the novel use of time since disturbance or assembly time rather than a static 'catchment' disturbance variable enabled us to investigate new aspects of the relative importance of neutral and niche community structuring processes. Network geometry and dispersal modalities interact in structuring populations therefore both factors need to be considered when investigating population processes in river networks (Chaput-Bardy et al. 2009). Because disturbance is ubiquitous in streams, studies of disturbance and community assembly in benthic ecology could contribute to wider ecology and apply to human or natural disturbances (Death 2010). While in this study disturbance at the network scale was used, there is potential for disturbance at smaller scales to interact with branching patterns (e.g. more disturbed around confluences, Benda et al. 2004, Kiffney et al. 2006) leading to different metacommunity processes in different parts of networks (Brown and Swan 2010). However, it remains to be determined whether parts of networks can act as sources and / or sinks for example, after disturbance or during restoration. Both disturbance regimes and habitat geometry (e.g. branching and connectivity) are frequently altered by humans. Therefore it is pertinent to investigate how habitat geometry and disturbance could interact (Starzomski and Srivastava 2007) to influence community structure in dendritic networks.

Acknowledgements

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"our job as scientists is arguably not to map the world onto our mental structures, but to re-wire our mental structures to reflect the world"

-- Palmer & White 1994

Chapter Four

Complementary limitations on stream macroinvertebrate community variability: effects of isolation and habitat characteristics

Abstract

Spatial processes structuring communities are difficult or impractical to investigate experimentally at large spatial scales. Therefore, statistical methods and novel survey approaches are needed to help understand how interactions between local environmental and regional dispersal processes affect communities. Treating effects of local and regional processes individually is often not useful, because they are interdependent, and nearly always statistically inseparable. Using quantile regression, I investigated factors limiting variation in adult and larval benthic stream macroinvertebrate community structure in four headwater stream networks on the West Coast of the South Island, New Zealand. I showed that both regional spatial effects (e.g. isolation, habitat size) and local environmental conditions (e.g. habitat structure, food resources) play different, but interacting roles in limiting variation in adult and larval benthic stream macroinvertebrate communities. Both adult and benthic aquatic macroinvertebrate communities showed marked decreases in variability with increasing habitat size. The upper limit to community variation was significantly related to local environmental factors, whereas the lower limit of community variation was significantly related to isolation of the communities. Although community variability detected in both larval and adult life stages was similar, community structure with respect to functional community isolation differed between adult and benthic macroinvertebrate community similarity. This suggested that spatial structuring processes such as different dispersal modes vary

between life stages, but result in the same variation in community structure observed. These results indicate the importance of joint limiting mechanisms on community composition, including processes associated with island biogeography and metacommunity theories. The limit response approach is likely to be particularly useful in overcoming challenges addressing the relative importance of local and regional processes structuring communities, especially communities in complex spatial arrangements such as dendritic networks.

Introduction

Regional and local processes work together to produce non-random community assemblages (e.g. McDowall 1996, Chave 2004, Thompson and Townsend 2006). Regional processes such as dispersal, colonisation and extinction are often considered stochastic processes and make up the theory behind neutral metacommunity models (e.g. Hubbell 2006, Leibold and McPeek 2006). In contrast, local processes are related to local environmental conditions and niche theories (e.g. Vandermeer 1972, Leibold and McPeek 2006) and can include local species interactions. Although both regional (dispersal) and local (environmental conditions) influences are important, it is difficult to determine their relative importance and how they interact to control community assembly, structure and variability. There is potential for processes such as dispersal, species interactions, colonisation, extinction and niche associations to change community structure in opposite directions (Driscoll and Lindenmayer 2009). This can result in failure to detect any significant patterns, or give unexpected results and therefore lower the predictability of community structure. Furthermore, the nature of interactions between potentially opposing processes is unknown and the importance of

one process may depend on a specific character of another. For example, Cooper (2010) found that the severity of effects of poor water quality on benthic communities depended on other stream conditions such as habitat complexity and disturbance. Lancaster et al. (2009) also found that stream communities were limited by food resources under certain dissolved oxygen (DO) conditions, but limited directly by DO in others. Thus, multiple sources of stress can have non-additive effects on communities, and it is possible that habitat associations may also be more important under certain dispersal scenarios, for example. Investigating this variability and predictability in community structure due to combinations of interacting factors is likely to provide valuable insights into the influences of local and regional processes on community dynamics.

Dendritic stream networks are spatially structured in a hierarchical manner, with small streams progressively flowing into larger streams. This directional structure and flow must have an influence on both dispersal processes and local in-stream conditions, but has rarely been addressed (Humphries and Ruxton 2002, Benda et al. 2004, Lutscher et al. 2007). Dispersal is a key life history trait for population processes as it contributes to gene flow, can prevent local extinction, and determines the probability of patch recolonisation (Chaput-Bardy et al. 2009). Understanding the influence of dispersal on community structure within a spatially structured system will greatly contribute to knowledge of how local communities are assembled.

Ecosystem size, distance between habitat patches, and local environmental conditions are key predictors in many theories such as island biogeography theory (Kadmon and Allouche 2007), niche theory (Vandermeer 1972) and metacommunity theories (Leibold et al. 2004) which attempt to explain species distribution in the environment. The spatial arrangement of habitats and the influence of this arrangement on community processes, incorporates

the physical distance between locations (Tuomisto and Ruokolainen 2008), habitat size and isolation (Kadmon and Allouche 2007, Economo and Keitt 2010). Thus, spatially explicit models need to combine the effects of habitat area, isolation, stochastic colonisation and extinction processes, habitat heterogeneity and niche partitioning to understand how they interact and influence community assembly. Furthermore, processes structuring communities within a network may change depending on habitat size, juxtaposition of habitats differing in size, and the types and the interplay between species, individuals and their dispersal (Fagan 2002, Grant et al. 2007).

Habitat size is both a local environmental characteristic and influences colonisation, which is a spatial, regional process. Thus habitat size integrates processes across community assembly theories. Considerable theory exists as to how habitat size influences stochasticity in populations and communities, particularly via extinction and colonisation processes (Hanski 1998, Connor et al. 2000, Kadmon and Allouche 2007). Because the chance that sites will be colonised diminishes with distance from a source of colonists (Suren and McMurtrie 2005), and large areas receive more colonisers than small ones (Connor et al. 2000, Kadmon and Allouche 2007), smaller habitats maybe more strongly influenced by stochastic events than larger, more deterministically influenced habitats (Kadmon and Allouche 2007). In addition, variation in population and community structure is predicted to increase with isolation, because isolation decreases immigration rates, increasing the likelihood of stochastic extinction (Kadmon and Allouche 2007, Driscoll and Lindenmayer 2009).

It has been hypothesised that headwater streams serve as refugia and source areas for biodiversity (Freeman et al. 2007, Wipfli et al. 2007), although theory suggests this is likely to be an oversimplification. Headwater locations should receive fewer migrants than sites further downstream as

colonisers cannot come from upstream and will either have to cross land or arrive from further downstream (Chaput-Bardy et al. 2009), leading to increased isolation and stochasticity in community structure (Kadmon and Allouche 2007, Economo and Keitt 2010). More realistically, larger, more connected sites are likely to be more important 'sources' than smaller more isolated ones (Economo and Keitt 2010). For example, confluences may act as 'hotspots' of biodiversity and as 'sources' in 'source-sink' community dynamics (Benda et al. 2004, Kiffney et al. 2006), being both larger and more 'connected' habitats than headwater reaches. The occurrence of various combinations of habitat size and isolation in dendritic networks, provides an ideal opportunity to investigate effects of habitat size and isolation on community structure.

In river systems, habitat size, isolation and the distance between habitat patches are spatially autocorrelated, with smaller streams near the headwaters converging into fewer larger downstream segments. Habitat size is often equated with stream order (e.g. Brown and Swan 2010) to simplify spatial relationships, although this is an overly simplistic procedure. First-order streams do not contain metacommunities independent from second order communities, and can flow into small or large second-order streams, and even third order streams, resulting in a range of potential influences on their community dynamics despite local size and habitat constraints.

Differences in the size of adjacent habitats within stream networks could lead to interesting movement dynamics between communities, particularly when different modes of dispersal are present (e.g. Cottenie 2005, Brown and Swan 2010). For example, the neutral metacommunity model predicts stronger changes with distance for communities that include a large proportion of poorly dispersing individuals (Brown and Swan 2010). Similarly, improved understanding of community dynamics should be gained by ex-

amining different dispersal modes among life history stages, even within species. For instance, many stream insects have a benthic larva restricted to the stream network, and a flying adult, which has the potential to leave the network and move within and between branches within stream networks. These very different, but interacting, dispersal mechanisms are likely to influence the outcomes of spatial interactions between communities but are rarely studied together or compared in studies of community assembly and structure. Considering the spatial and dispersal patterns of both adult and benthic life stages in a stream network, should result in better ability to interpret spatial and environmental processes that interact to structure communities.

The strong covariation between environmental and spatial structure found in nature makes it difficult to discriminate between local niche and other spatial processes (Legendre 1993). Therefore, because multiple interacting factors control community structure, a useful approach might be to examine limit responses rather than central mean responses (Cade and Noon 2003, Lancaster et al. 2009, Cooper 2010). Hypotheses are usually fitted about central tendencies such as means, however when fitting central relations, other independent variables can affect the dependent variable simultaneously, creating variation that often results in poor model fit (Downes 2010). When integrating regional and local process models, it is likely to be more informative to test hypotheses about limits on the distribution of organisms and what constrains variation in communities rather than focussing on 'average' responses.

In this study I used quantile regression to test factors limiting variation in adult and larval macroinvertebrate community structure of streams. I tested whether predictability of macroinvertebrate community structure was linked with habitat size, isolation, local environmental conditions, and

neighbouring communities, and therefore whether communities in different parts of stream networks were controlled by different factors. I hypothesised that variability in community composition would change with local habitat size, indicating that structuring processes would also differ between locations in a stream network. Specifically, I predicted that small streams would have more variable community structure, their small habitat size, local environmental factors, isolation, and neighbourhood effects having major effects. To further tease out the importance of neighbouring communities to local community processes, the similarity of neighbouring community structure was assessed with respect to distance from local communities and local habitat size. I hypothesised that community similarity to the closest neighbouring community would increase with local habitat size.

Methods

Macroinvertebrate sampling of stream networks

Four headwater stream networks on the West Coast of the South Island, New Zealand were selected with up to 19 sampling sites on each network to capture spatial processes (Figure 1). Sampling sites were 30 m long reaches located on each tributary and on the mainstem between tributaries. Larval benthic macroinvertebrates were sampled at each of these sites in January or February 2008; adults in November or December 2008. To sample benthic macroinvertebrate communities, three Surber samples (0.06 m^2, 250 μm mesh) were taken randomly from riffles and preserved in 70% ethanol. Light traps were constructed from garden lights adapted with UV-LEDs (black light, 395 – 400 nm, a wave length known to attract adults of many aquatic invertebrates; Collier et al. 1997) placed in the centre of white plastic trays (24 x 35 x 7 cm; Figure 1). Three replicate traps were set up on the stream

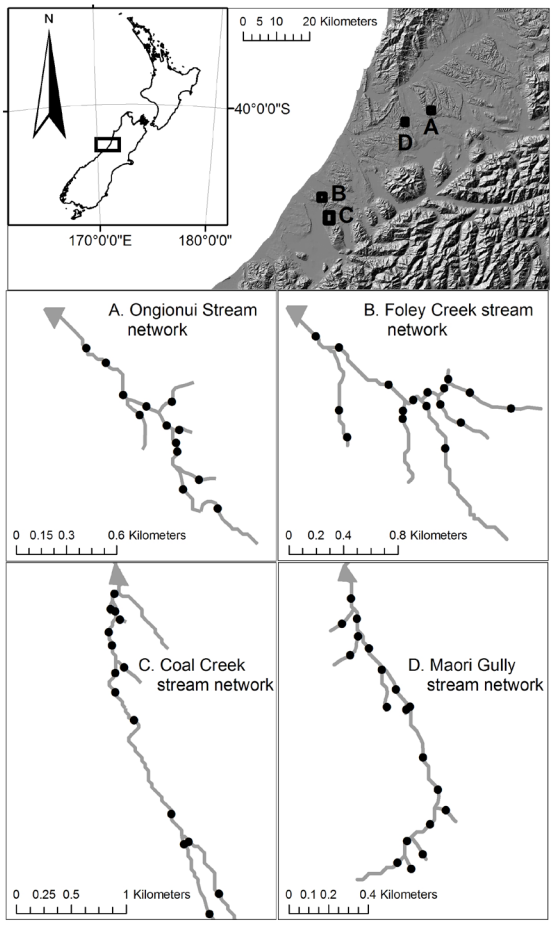

Figure 1. Four headwater stream networks (A-D) on the West Coast of the South Island of New Zealand were sampled for larval and adult benthic macroinvertebrate communities using Surber samplers and UV-light traps adapted from a garden light placed over a white tray (E). Sampling sites are indicated by circles and stream flow by arrows.

E.

banks at each of the sites sampled for benthic macroinvertebrates and left for 4-5 days with the light on constantly. A small amount of detergent, water and ethanol were placed in the trays to break the water surface tension, trap, and preserve invertebrates. Traps also had chicken wire covers (2.5 cm mesh) to protect them from interference by weka (*Gallirallus australis*), a local ground-dwelling bird. Light traps were most successful in attracting and capturing Trichoptera. Hence, analyses were confined to this order. Because light traps in Ongionui Stream were damaged by flood waters, data from them were not included in analyses.

Distance measures

Traditionally, Euclidean (straight line) distance is used as a distance measure to illustrate spatial patterns between sites. However, distance between sites along the course of the stream (i.e. stream distance), may be more appropriate for representing ecological spatial pattern in streams (Grant et al. 2007, Peterson et al. 2007) and was used in this study. Pair-wise stream distance matrices between all sites were calculated in ArcGIS (OD-cost matrix tools; ArcMap 9.2).

Macroinvertebrate community structure

Benthic macroinvertebrates were sorted, counted and identified under a dissecting microscope at 10 – 30 x magnification. Immature aquatic macroinvertebrates were identified to genus or species using keys in Winterbourn et al. (2006). Average abundance data (square root transformed) were analysed using Non-metric multi dimensional scaling (NMDS) in PRIMER (v. 5; Clarke and Gorley 2000), producing measures that represented differences in community composition across sites along the ordination axes. Male adult Trichoptera were identified to species level (Neboiss 1986, Johanson 1999, Ward 2001; M.J. Winterbourn, pers. comm). Because not all females could be identified to species level (Neboiss 1986) they were disregarded. Analyses were then conducted on the average abundance of males per trap day (square root transformed). Male Trichoptera data were also subjected to NMDS, to produce equivalent community measures to those obtained for benthic invertebrates.

In addition to the NMDS community scores, similarity matrices were constructed for benthic and adult macroinvertebrates. A similarity matrix

Table 1. Definitions of key predictor variables for stream macroinvertebrate communities used in the study.

Definitions of predictor variables	Description	Details of values
Local environmental conditions	Set of local habitat and resource variables (Table 2)	Ordinated using NMDS* to represent variation in environmental structure
Isolation	Area of potentially available stream habitat within a 150 m buffer around each site (Figure 2)	Small values indicate increased isolation
Similarity to closest site (functional isolation)	Community similarity between a site and its closest neighbouring site (along the stream) (Figure 3)	Similarity was expected to increase with local and neighbour habitat (stream) size due to mass effects
Local habitat size	Average wet width of stream reach measured in the field (m)	
Neighbour habitat size	Average wet width of closest neighbouring site (m)	For graphical representation this was local width - neighbour width + 4, to enable the display of differences in habitat size between neighbours

*Non-metric multidimensional scaling

(Bray-Curtis similarity) was calculated separately for each network in PRIMER and used to measure variation in community structure between neighbouring sites (Table 1, Figure 2).

Local environmental variables

A range of local environmental variables were sampled over each 30 m site reach on each network. These included measures representing habitat structure, flood disturbance and macroinvertebrate food resource availability (Table 2). Local habitat size (average wet width of stream reach) was not included in the 'habitat' data set, as I wanted to test hypotheses related to local habitat size and isolation independently. A NMDS was carried out on the suite of environmental variables to reduce them to a composite measure to represent local environmental conditions relevant to macroinvertebrate communities.

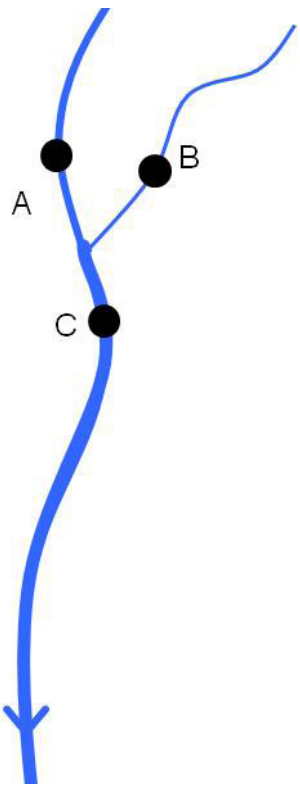

Figure 2. A measure of functional habitat isolation based on community similarity and physical distance between communities was used to investigate processes influencing local community variability. The thickness of the lines making up the stream network represent local habitat size and circles represent sites. The extent of similarity between close sites was expected to increase with local habitat size. For example, if sites A, B and C are equidistant from each other along the stream, both A and B should be more similar to site C (than to one another), due to the larger local habitat size of site C (i.e. A is more similar to C than it is to B, and B is more similar to C than it is to A, even though the distance A to B is no less than A to C or B to C).

Table 2. Local environmental conditions measured at each site and used as input for the non-metric multi dimensional scaling ordination to provide a composite score for environmental conditions to relate to stream macroinvertebrate communities.

Variable	Units	Comment	Reference
Disturbance (upper)		Pfankuch disturbance score total for the upper stream banks	
Disturbance (lower)		Pfankuch disturbance score total for the lower stream banks	Pfankuch (1975)
Disturbance (bed)		Pfankuch disturbance score total for the stream bed	
Disturbance (total)		Total of upper, lower and bed Pfankuch disturbance scores	
Avg particle size	mm	Mean length of longest axis of 50 particles on stream bed	Gordon et al (1992)
Min particle size	mm	Minimum length of longest axis of 50 particles on stream bed	
Max particle size	mm	Maximum length of longest axis of 50 particles on stream bed	
Range particle size	mm	Range in length of longest axis of 50 particles on stream bed	
pH		Spot measure using a hand held meter name the ph meter	
Avg depth	cm	Mean from three depths across the stream at four points along the 30 m stream reach	
Min depth	cm	Minimum of three depths across the stream at four points along the 30 m stream reach	
Max depth	cm	Maximum of three depths across the stream at four points along the 30 m stream reach	
Range depth	cm	Range of three depths across the stream at four points along the 30 m stream reach	
Avg velocity	m/sec	Average of three velocities taken over a 10 m section of stream	
SRP	µg/L	Soluble reactive phosphorus from water samples filtered in the field and frozen before analysing	
Conductivity	µs	Spot measure using a hand held meter name meter	
Water temperature	˚C	Spot measure using a hand held meter name meter	

Table 2 (continued)

Variable	Units	Comment	Reference
CPOM	g/0.06m^2	Ash free dry mass of coarse particulate organic matter (>1 mm) collected in a 25 x 25 cm Surber sampler	Hauer & Lamberti (1996)
FPOM	g/0.06m^2	Ash free dry mass of fine particulate organic matter (250 µm-1 mm) collected in a 25 x 25 cm Surber sampler	
Bryophyte (dry mass)	g/0.06m^2	Ash free dry mass of bryophytes collected in a 25 x 25 cm Surber sampler	
Canopy cover	%	Mean percentage of canopy cover estimated from three digital photographs (ArcSinSqrt transformed)	
Pool	%	Percentage of 30 m reach in pool habitat	
Riffle	%	Percentage of 30 m reach in riffle habitat	
Run	%	Percentage of 30 m reach in run habitat	
Cascade	%	Percentage of 30 m reach in cascade habitat	
Backwater	%	Percentage of 30 m reach in backwater habitat	
Leaf	%	Percentage of 30 m reach with leaf cover in the stream	
Wood	%	Percentage of 30 m reach with wood cover	
Bryophyte (%)	%	Percentage of 30 m reach with moss cover	
Macrophyte	%	Percentage of 30 m reach with macrophyte cover	

Local habitat size and spatial variables

Along with the field measure of local habitat size at each sampling site, I created an isolation metric using ArcGIS (ArcMap 9.2). This isolation measure was the area of stream (i.e. potential larval macroinvertebrate habitat) within a certain area calculated using a 'buffer zone' approach adapted from methods of measuring isolation in terrestrial ecosystems (Driscoll and Lindenmayer 2009). This involved taking stream reach widths measured in the field and applying them to the corresponding stream reaches in GIS using buffering techniques, to obtain a size-specific stream network in the GIS framework. The 'buffer zone' was a circle 150 m in radius around each site with an inner area of 20 m radius removed from the total buffer, to remove the effect of 'local' habitat size, which was of interest in itself, thus resulting in a 'donut' shaped buffer (Figure 3). The 150 m radius was chosen to be a reasonable distance for relatively frequent dispersal by individuals but not put too much emphasis on relatively rare long distance flight (Miller et al. 2002, Petersen et al. 2004). The 20 m radius (40 m diameter) is reasonable as a local habitat area as it encompasses the 30 m sampling reach and benthic invertebrates have been recorded moving up to about 13 m / day (Elliott 2003). This isolation measure is obviously simplified, but it is impossible to get a single ideal measure of isolation over multiple scales in a complex spatial structure (Bohonak and Jenkins 2003, Economo and Keitt 2010). Within this 'buffer donut', the total area of stream habitat was calculated (sometimes including, for example, nearby tributary habitat), resulting in a measure of potentially suitable habitat area for larval stream macroinvertebrates surrounding each site (Figure 3). This was used as a metric of isolation for each site; for example, the more stream area within the 'donut' around the site, the less isolated the site (Table 1). Isolation is difficult to assess in dendritic stream networks (Economo and Keitt 2010),

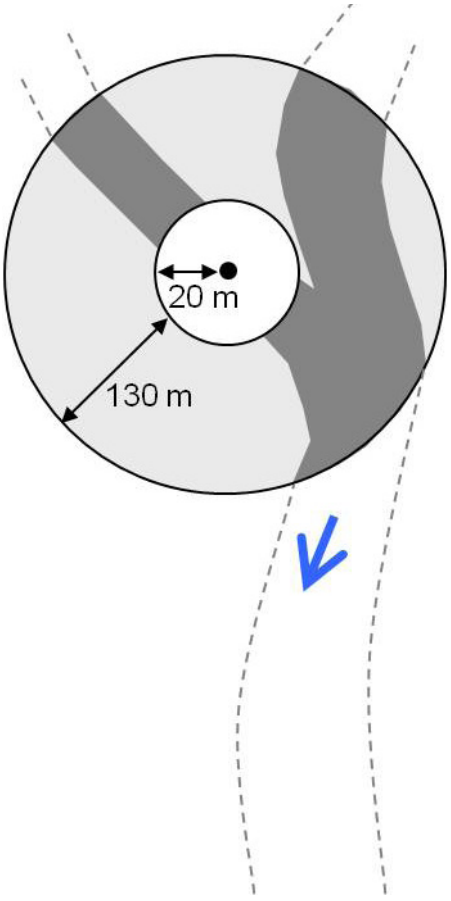

Figure 3. Habitat isolation was calculated as the area of stream (dark grey shaded area) within a 150 m radius circular buffer around each sampling site. Grey shaded area (light and dark) represents the 'buffer' area within which the stream habitat area (dark grey) was calculated to measure the amount of aquatic habitat surrounding a site, and therefore represented an index of isolation. The immediate area within a 20 m radius surrounding each site (white area) was excluded from the isolation area metric to avoid confounding with local habitat size, resulting in the shaded 'donut' shape. The arrow indicates the direction of stream flow.

despite the fact that buffers are regarded as useful measures of patch isolation in fragmented terrestrial ecosystems (Driscoll and Lindenmayer 2009). Although my buffer-based measure does not take into account directional isolation due to downstream flow effects, it does capture important aspects of isolation such that larger streams with more habitat within the buffer (less isolated) will also be the ones downstream and therefore more connected by flow. Therefore, the position of a site in the stream network was captured both by local habitat size and the buffer-based measure of isolation.

Because I was interested in the effect of the juxtaposition of different sized streams on community composition, I calculated the difference in local habitat size measured in the field, between adjacent sites (local size

minus neighbour size). I added four (the lowest constant to get positive numbers) to each of these differences to get positive metrics for graphical representation (Table 1).

Quantile regression

To test whether variability in community structure changed with local habitat size, and hence position in the stream network, I fitted linear functions to the upper and lower limits of relationships between measures of community structure (ordinations of both adult and benthic macroinvertebrate community composition) and local habitat size, using quantile regression in R ('quantreg' package; Cade and Noon 2003, R Development Core Team 2007, Koenker 2009) (I refer to these relationships as 'community-habitat size' relationships). I also tested whether environmental or isolation factors were related to these limits by investigating limit responses for both environmental structure (ordination scores) and isolation metrics when related to local habitat size. To further test whether communities at the upper and lower limits of variability in community structure could be driven by environmental or isolation factors, the sites that fell within upper (90^{th}) and lower (10^{th}) quantiles of the initial community-habitat size relationships were regressed against the environmental and isolation variables. Confidence intervals were computed by the rank inversion method and P-values by bootstrapping (Koenker 2009, Cooper 2010).

Results

Community variance and local habitat size

Community structure of both adult Trichoptera and benthic macroinvertebrate communities was more variable in smaller streams than larger streams

(Figure 4). The relationship between local habitat size and both benthic (axis 2 from NMDS) and adult (axis 1 from NMDS) community structure had significant negative ceiling, and significant positive floor, limit responses (Table 3). Original NMDS figures are available in Appendix F. Quantile regression of these relationships indicated fitted slopes significantly different to zero for 90th and 10th quantiles (Table 3). Species lists are available in Appendix A (benthic) and Appendix G (adult).

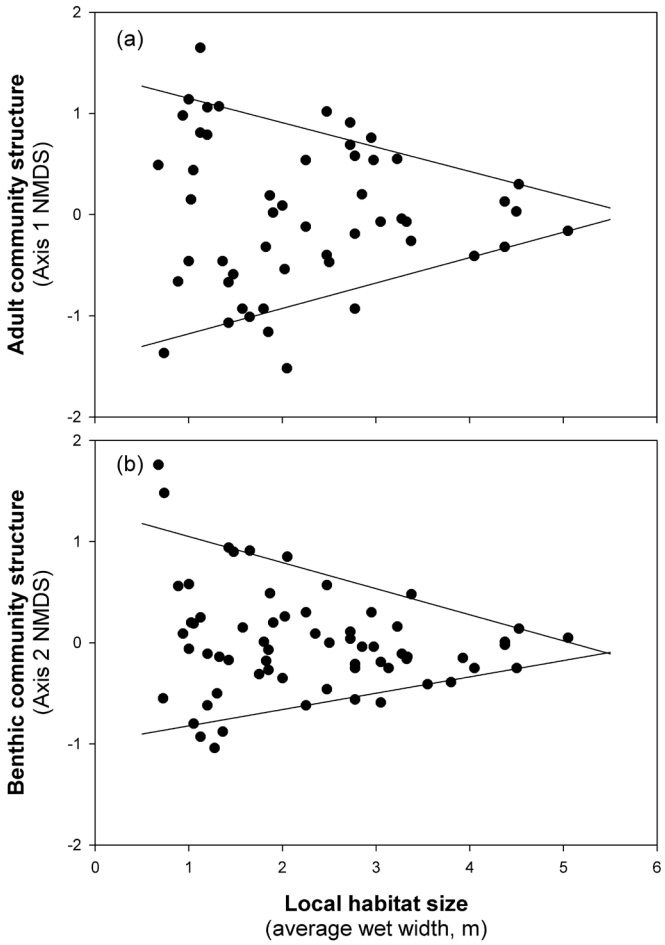

Figure 4. Quantile regression relationships between local habitat size and (a) adult Trichoptera assemblages, and (b) benthic macroinvertebrate community composition. 90th (upper) and 10th (lower) quantiles are indicated.

Environmental and isolation drivers of community structure limits

Environmental structure (NMDS axis 2) had a significant negative upper limit relationship with local habitat size (Table 3, Figure 5a). This suggests that the upper limit response for macroinvertebrate communities (Figure 4) may be related to the environment-habitat size relationship. There was also a significant relationship between the community scores from the upper 90th quantiles (Figure 4) and their corresponding environmental structure axis 2 scores for both adult (Figure 5b) and benthic (Figure 5c) communities. This relationship provides further support for a habitat size-environment-invertebrate community relationship at the upper limit of variation in community composition and shows that upper limit variation in macroinvertebrate community composition could be explained by environmental drivers.

Table 3. Results of quantile regressions, where local habitat size was the predictor variable for each response variable in column one. Values highlighted in bold were significant ($\alpha < 0.05$) when assessed using bootstrapping methods.

		Coefficients	
Response	**Quantile**	**Intercept**	**Slope**
Adult Trichoptera community – NMDS* axis 1	Upper 90th	**1.39**	**-0.24**
	Lower 10th	**-1.43**	**0.25**
Benthic community – NMDS axis 2	Upper 90th	**1.31**	**-0.26**
	Lower 10th	**-0.98**	**0.16**
Environmental NMDS axis 2	Upper 90th	**0.92**	**-0.25**
Isolation	Lower 10th	38.14	**262.92**
Benthic - similarity to closest site	Lower 10th (part of data)	**29.18**	**10.58**
	Linear regression (part of data)	**12.70**	**9.72**

*Non-metric multidimensional scaling ordination

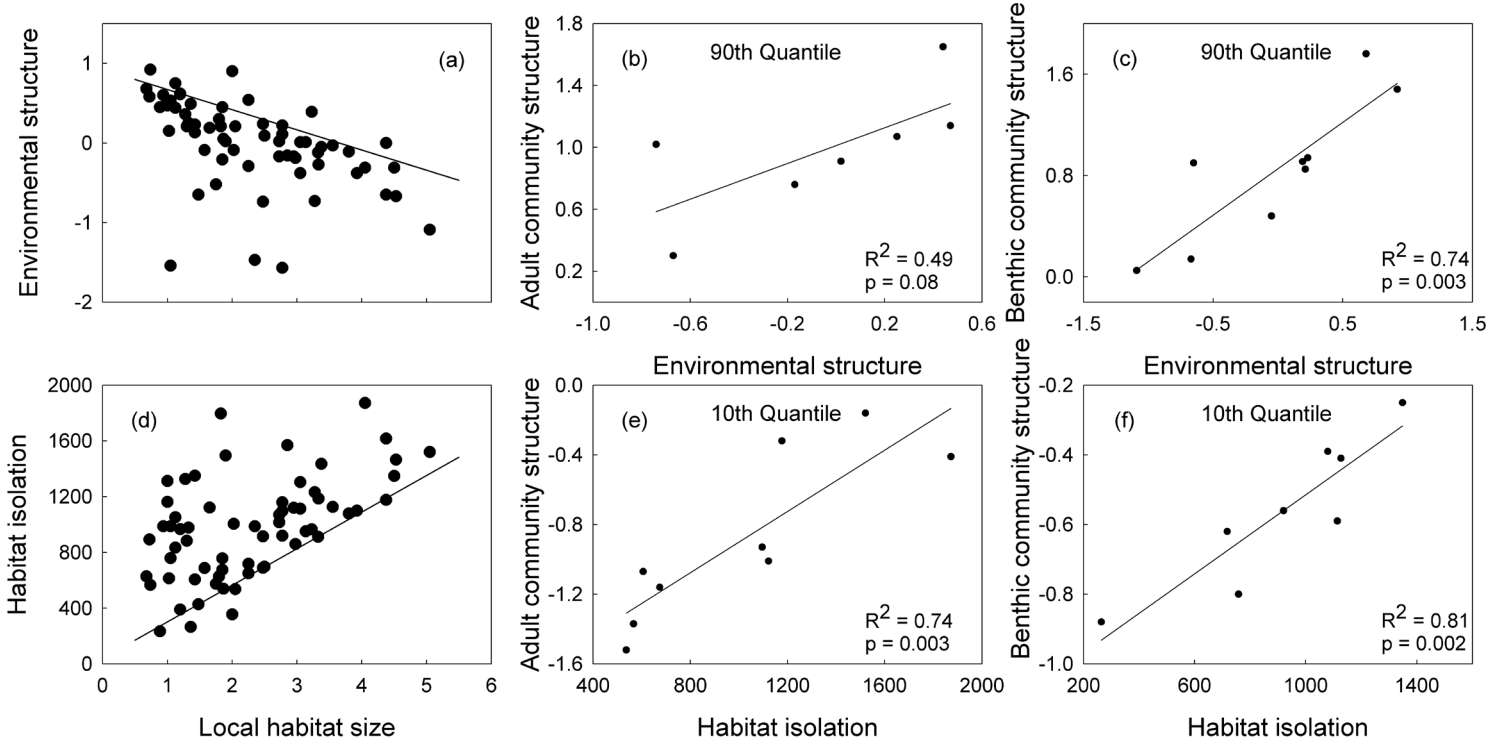

Figure 5. Local habitat size (average wet width, m) had an upper limit response with (a) environmental structure (axis 2 NMDS), and a lower limit response with (d) isolation (area of stream habitat in buffer, m^2). Adult Trichoptera (axis 1 NMDS) (b) and larval benthic macroinvertebrate (axis 2 NMDS) (c) communities within the 90th quantile were related to environmental structure. In the lower 10th quantile both adult (e) and benthic (f) community structure were related to isolation. Environmental structure, adult and benthic communities were all multivariate measures of their relative structure from non-metric multidimensional scaling ordinations.

In contrast, isolation had a significant positive lower quantile limit in relation to local habitat size (Table 3, Figure 5d), suggesting that the lower limit of the community variation response to local habitat size could be driven by isolation effects. A habitat size-isolation-community structure relationship was further supported by significant relationships between isolation and both adult and benthic macroinvertebrate communities within the lower 10th quantiles of Figure 4 (Figure 5e and f).

Functional isolation

'Similarity to the next closest site' of benthic macroinvertebrate communities showed a significant positive lower limit response to local habitat size, with an increase in community similarity with an increase in local habitat size (Figure 6a, Table 3). This was not a simple exclusion zone relationship, however, but had parallel lower limits indicating another factor was also involved in limiting community structure (Cade and Noon 2003). When differences in habitat size between a local site and its neighbour site were taken into account (size of circles, Figure 6), sites that were larger than their neighbours by approximately 1.5 m wet width (larger circles belonging to the lower parallel line, Figure 6) were less similar for their given size, indicating neighbour size as an additional limiting factor. Adult Trichoptera community composition did not show the same pattern, however, with no discernable pattern of community similarity to the closest site with local habitat sizes (Figure 6b).

Discussion

I have shown that variation in community composition decreased with increasing local habitat size, both for adult Trichoptera and benthic

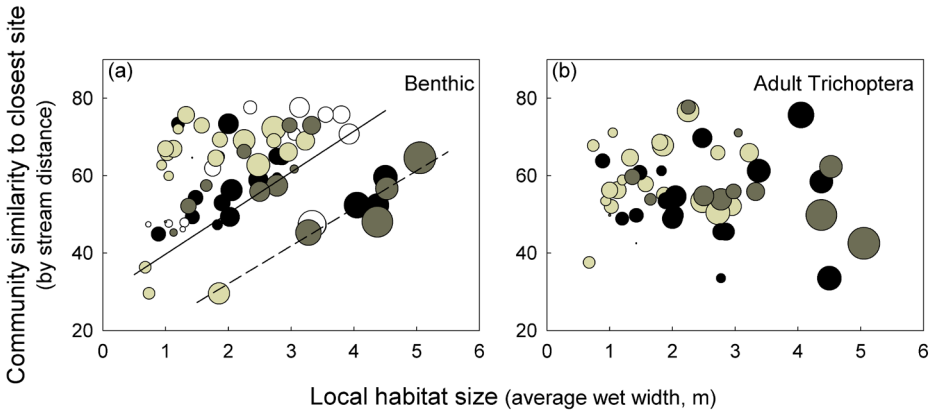

Figure 6. Community similarity of a local site to its nearest neighbouring site in relation to local habitat size in (a) adult Trichoptera assemblages, and (b) benthic communities. The larger the circles, the larger the size of the local site habitat compared to its neighbour. The small circles represent sites that are smaller than their neighbour, whereas medium-sized circles represent neighbouring sites comparable in size. The shading of the circles indicates the stream network (black = Foley Creek, dark grey = Coal Creek, light grey = Maori Gully Stream, white = Ongionui Stream; adults were not sampled at Ongionui Stream). The dashed regression line corresponds to the sites that were larger than their neighbours by at least 1.5 m, while the solid regression line is the lower 10th quantile limit for the remaining sites.

stream macroinvertebrates. This habitat size-related community variance was associated with both local environmental heterogeneity and spatial processes. This reveals, for the first time in stream systems, complex interactions between habitat size, local environmental conditions, isolation and neighbourhood relations in explaining variation in aquatic macroinvertebrate community composition.

Habitat size and variability in community structure

I hypothesised that community variability would differ in different locations within dendritically structured stream networks. To represent location in the stream network I combined continuous measures of habitat size and isolation. I also expected spatial community interactions between stream orders, as they are usually adjacent habitats. Similar patterns in

community structure were detected for both adult trichopterans and benthic macroinvertebrate communities, with more community variation in smaller than larger streams. I found a marked pattern of community change with habitat size; community structure had both an upper and lower limit linked to habitat size. As streams got larger, community composition converged between sites, indicating that larger streams were more deterministic in community structure. Thus, the processes structuring these communities changed with respect to the location in the network. I discuss mechanisms underlying these patterns of community variability below.

What is it about habitat size that drives the variability in community structure?

Habitat size itself could be used to explain the detected changes in variance using island biogeography and species-area theories (e.g. Kadmon and Allouche 2007). For example, habitat size can control species-area relationships that influence colonisation, extinction and encounter rates of colonists (Connor et al. 2000, Kadmon and Allouche 2007). Small populations (often small due to limited habitat) are also more likely to go extinct due to chance (Kadmon and Allouche 2007). However, while local habitat size was an obvious limiting factor at both upper and lower quantiles of community composition, it is unlikely that 'habitat size' per se was the only driver of community structure. Rather, other processes affected by habitat size were likely to be indirectly influencing community structure, as has been previously shown by Blakely and Didham (2010). The 'local habitat size' variable captures many interacting factors driven either by habitat size or correlated with habitat size. The relationships between habitat size and associated processes are especially confounded in stream networks due to their dendritic network structure and the directional, hierarchical nature of

hydrological, geomorphological and biological resource flows. Habitat size could also be indirectly controlling processes such as species interactions and / or habitat associations leading to increased stochasticity in communities in smaller streams. In my study, the presence of clear upper and lower limits of community structure with habitat size, suggests it is not unreasonable to suspect that an interaction between regional (extinction, colonisation) and local (habitat, species interactions) processes simultaneously driving or limiting community variability. Interactions between local and regional community structuring factors are relatively common (e.g. Cottenie 2005, Thompson and Townsend 2006), however these have not previously been considered alongside habitat-size related concepts.

Local environmental conditions driving community variation? – not entirely

Investigating the potential interaction of local and regional factors, I found that local environmental conditions alone, could not account for all of the variation in community composition. I showed that at least the upper limit of variability in both adult and benthic macroinvertebrate communities was habitat-related, as there was a strong relationship between community structure and local environment in the upper quantiles. Therefore one of the limiting variables controlling community variation is likely to be set by local environmental factors. Previous studies have independently shown the importance of environmental limits (Lancaster et al. 2009, Cooper 2010) and that environmental community drivers should be more important in smaller than larger streams (Brown and Swan 2010), however they did not consider environmental limits and habitat size as interacting factors. In my study, environmental variables appear to be drivers, not for communities within particular habitat size classes, but for the limit of particular community structure, related to local habitat size.

Isolation driving community variation? – not entirely

Isolation has been hypothesised to greatly influence stochasticity of communities due to variability associated with colonisation and extinction cycles (Driscoll and Lindenmayer 2009, Economo and Keitt 2010). Habitat isolation had a lower limit response with local habitat size, with larger streams being less isolated than smaller ones (Figure 5d). However, the level of habitat isolation of smaller streams was more variable (Figure 5d), potentially leading to the community variation I also detected at these smaller sites. My measure of habitat isolation was significantly related to community structure for both adult and benthic macroinvertebrate communities, but again only at the lower limits of the community-habitat size relationship (i.e. the lower limits in Figure 4). Therefore, isolation can limit community composition in combination with local habitat size conditions.

Local environmental conditions and isolation work together to produce variance in communities

One of my main conclusions is that community variation can be limited by both local environmental and regional dispersal processes (e.g. isolation). In itself, this finding is not new, but through a novel approach I was able to demonstrate interactions between local environmental and regional dispersal processes rather than separating them, e.g. partitioning the variance between the two (Legendre et al. 2005, Smith and Lundholm 2010). Whereas Driscoll and Lindenmayer (2009) suggested that various combinations of local and regional processes can lead to conflicting spatial patterns, resulting in a lack of strong pattern because of cancelling effects, I found that rather than cancelling each other out, different processes interacted to limit variability in community composition. Using a traditional central tendency approach, I would have produced misleading results, however using quantile

regression to model neutral and niche processes simultaneously meant I could detect and investigate interactions between multiple interacting drivers. More specifically, the effects of isolation and local environmental conditions on communities, differed depending on habitat size and therefore position in the network, but were only detected at the limits of community variability. Although both Driscoll and Lindenmayer (2009) and Brown and Swan (2010) predicted that increasing isolation should result in stronger environmental associations, I found that the more stochastic communities were not necessarily associated more strongly with environmental factors. Environmental associations with communities occurred over the whole spectrum of stream sizes, though only where environmental factors were limiting. This meant a range of habitat conditions appeared to be 'good enough' for many different species combinations.

Neighbourhood considerations and functional isolation

When considering community structure at a finer spatial scale, I wanted to know if more variance in community composition could be explained by examining detailed neighbourhood dispersal. Small scale spatial linkages between local and neighbouring sites are likely to be important for determining local species composition (Sanderson et al. 2005, Economo and Keitt 2010). I found that small streams in the mid-quantiles had more similar species compositions to large streams, suggesting local neighbourhood influenced community structure. This means that when small sites are not isolated, they have the potential to support communities more similar to those of comparatively larger streams. This finding is predicted theoretically by metacommunity theory, mass effects, source-sink, rescue effects and recent theory on isolation in networks (Economo and Keitt 2010). For benthic communities, I found community similarity to a neighbouring site

generally increased with local habitat size, while the resulting parallel lines on Figure 6a indicated an unmeasured limiting factor at some sites (Cade and Noon 2003). This factor turned out to be an interaction between local habitat size and the differences in habitat sizes between neighbouring sites. Thus, when a stream was larger than that of a neighbouring site beyond a certain threshold, communities were less similar than expected for the given local habitat size. Surprisingly, the same slope relationship was maintained between the sites that were larger than their neighbours by this threshold, and other sites at the lower limit of the community similarity relationship, i.e. the increase in community similarity with local habitat size was the same, although overall similarity was less.

The adult Trichoptera assemblages did not show these same community similarity patterns, however, suggesting that different spatial processes were structuring them. Because taxa vary in their dispersal abilities, importance of the community composition of the neighbouring site in influencing local community structure is also likely to vary with dispersal ability (Sanderson et al. 2005, Economo and Keitt 2010). The differences observed in neighbourhood effects between adult and benthic communities could therefore be a consequence of differing dispersal modes. Whereas benthic macroinvertebrates have limited opportunities to disperse, winged adults can potentially move further away. Because neighbourhood effect mechanisms can act in different ways and at different scales (Economo and Keitt 2010), they contribute to the local habitat size-related variance in community structure. Moreover, because adult and benthic macroinvertebrate communities had similar local habitat size-variance relationships (Figure 4), it begs the question as to whether, and how much, adults have the potential to influence benthic communities and vice versa.

Unifying local environmental and regional dispersal processes via habitat size and limit responses

Another important conclusion is that the complex branching spatial structure of stream networks has fascinating implications for both regional and local processes that structure aquatic macroinvertebrate communities. I detected effects of spatial network configuration and local habitat size on community variability. I addressed both regional (spatial) and local (habitat) community influences simultaneously. By concentrating on the influences of neighbouring communities, and by taking a more flexible approach than simply categorising sites by stream order, I was able to show that variation-producing mechanisms and limit responses interact to produce stochasticity and predictability in stream network communities. I found that both adult and benthic life stages had the same community variability structure with habitat size, but potential mechanisms driving this, varied between life stages. This finding raises questions as to the relationship and importance of drivers at different life history stages and how each life stage interacts with the other to influence spatial patterns of macroinvertebrate communities in stream networks. Thus there is much to be learnt about how different life stages of organisms with complex life cycles contribute to spatial community structure.

There is a general assumption in much of the literature that processes in headwaters and upstream reaches influence downstream processes disproportionately, and that therefore headwaters should be protected preferentially as 'sources' of species diversity (Vannote et al. 1980, Freeman et al. 2007, Wipfli et al. 2007, Death and Collier 2010). Although this down stream effect may be true for some processes such as leaf litter resource transfers (Vannote et al. 1980), it needs to be recognised that larger streams also influence small streams and can be 'sources' of fauna for small stream communities. Larger

streams can be more 'stable' or 'predictable' in terms of their invertebrate community composition as found in this study, whereas the species composition of small streams can be highly stochastic and therefore, although they could provide some colonists, they have variable reliability as 'sources' to maintain viable metacommunities over time. These findings suggest we need to embrace more encompassing concepts for community organisation when, for example, prioritising sites for conservation or management action.

The change in variability in community composition among locations through the stream network also has implications for statistical spatial analysis. Many standard spatial analyses (Mantel, variogram, etc) assume stationarity, i.e. that processes and variance are constant over the spatial area of investigation (Ganio et al. 2005), whereas this is usually not the case in stream networks. Therefore, to advance understanding of spatial processes influencing stream network communities, methodological, theoretical and empirical studies are still very much needed, as there are many complex interactions that may behave unexpectedly due to this special spatial arrangement of habitat. The limit response approach used in this study is likely to be particularly useful in overcoming these challenges.

Acknowledgements

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“all models are wrong, but some are useful”

-- G.E.P. Box

Chapter Five

Networks, neighbourhoods and community assembly: insights from macroinvertebrate communities in streams

Knowledge of the spatial structure of communities is key to understanding many ecological processes from small scale (e.g. individuals, genetics) to large scale (e.g. populations, communities) levels of ecological organisation (Grant et al. 2007). Patchy distributions and non-random assemblages of species are common in ecological systems (e.g. Heino 2005, Talley 2007, Ellwood et al. 2009), and how these patches interact is important for determining persistence, resilience, stability, foodweb interactions and ecosystem function (e.g. McCann et al. 2005). Understanding the spatial and temporal interactions between communities in these habitat patches is therefore imperative for both theoretical and applied ecology. Furthermore, many species making up a local community are likely to be influenced by processes at different spatial scales (Resetarits 2005). Thus, the spatial structure of habitats can influence community assembly at both local and regional scales.

Networks are by definition special spatial arrangements. Network properties have been used successfully to increase the understanding of food webs (e.g. Grant et al. 2007), and consideration of habitat networks have informed studies of terrestrial habitat fragmentation (e.g. Bodin and Norberg 2007) and ponds (e.g. Urban 2004). Most ecological network research has been in these 'lattice' networks where habitats or species are present at nodes (Figure 1a). Stream networks have previously been considered with a longitudinal spatial perspective (e.g. Vannote et al. 1980), but a shift from this linear view (Figure 1b) toward a more integrative spatial approach involving an appreciation of dendritic network structure where habitat can be both on the

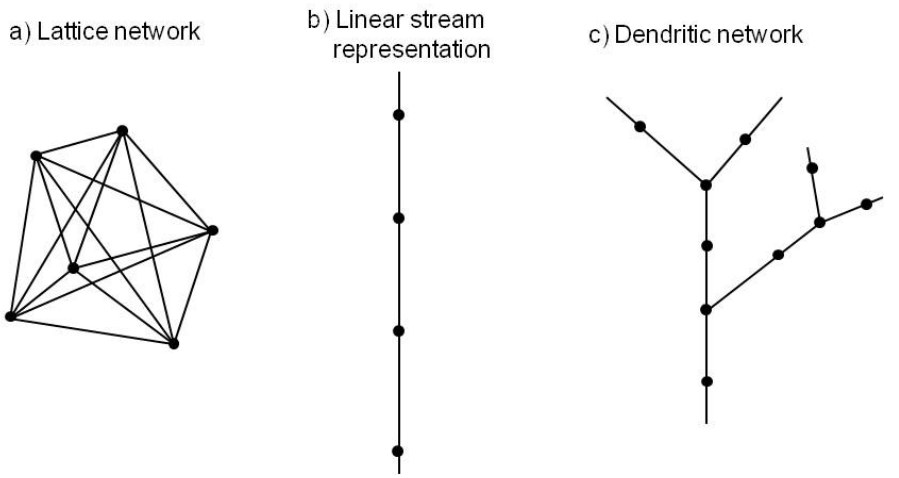

Figure 1. The lattice network (a) often used for spatial studies in terrestrial or lake systems. This spatial structure has sometimes been applied in streams (e.g. Thompson and Townsend 2006), but does not incorporate many aspects of dendritic network structure (e.g. direction of flow, branching pattern). Simplified linear views (b) have also been used to model longitudinal spatial patterns in streams (e.g. Vannote et al. 1980), but these do not take tributaries into account. The dendritic network (c) best represents spatial and functional processes in stream networks, where habitat can be nodes or branches and the hierarchical nature of tributaries is incorporated. Particular habitats / communities are indicated as black circles in the diagram, but in streams all branches could potentially be habitat.

branches and at nodes (Figure 1c), could increase understanding (Lowe et al. 2006, Clarke et al. 2008). Dendritic networks also have different levels of connectance between habitats compared to lattice networks (Labonne et al. 2008), and more potential dispersal directionality, particularly when movement is restricted to the network (Grant et al. 2007).

Dendritic networks are found in a number of systems such as rivers, planted windbreaks, riparian vegetation, roads and hedgerows (Holl and Crone 2004, Muneepeerakul et al. 2007, Groot et al. 2009, Morrissey and De Kerckhove 2009, Rodriguez-Iturbe et al. 2009). Incorporating the hierarchical structure of dendritic networks into ecological studies will enable a more complete understanding of the mechanisms and consequences of ecological processes and species-ecosystem linkages across spatial scales

in these important habitats (Lowe et al. 2006). Empirical research on dendritic network systems is still in its infancy, although there have been significant recent advances in theoretical studies such as those on connectivity and extinction processes (e.g. Fagan 2002, Labonne et al. 2008), and also conceptual and hypothesis generating studies of dendritic networks (e.g. Lowe et al. 2006, Grant et al. 2007, Clarke et al. 2008). Testing new theoretical advances on a wide range of dendritic populations and communities is essential if we are to advance understanding of community structuring processes in these systems. Important insights have come from studies of processes in dendritic networks for water chemistry (e.g. Peterson and Ver Hoef 2010), physical habitat character (e.g. Benda et al. 2004, Wallis et al. 2008), salamander (Grant et al. 2009), fish (e.g. Hitt and Angermeier 2008, Coté et al. 2009), and invertebrate populations and communities (Stewart-Koster et al. 2007, Heino 2009, Brown and Swan 2010, Clarke et al. 2010). However, there remains considerable scope for considering geometry and network architecture in formulating and testing hypotheses about species distributions, spatial processes, local habitat conditions, disturbance regimes, and for designing spatial sampling strategies (Clarke et al. 2008). There is also a need for knowledge of potential metacommunity dynamics such as source-sink dynamics and how sources and sinks are distributed in dendritic networks (Lowe et al. 2006, Woodford and McIntosh 2010) to help manage populations and ecological function in streams.

Spatial community dynamics of invertebrates in dendritic networks, such as metacommunity dynamics, are particularly interesting due to the complex dispersal pathways potentially involved. Therefore studying stream networks will be useful for increasing understanding of complex spatial community dynamics. For example, the majority of stream insects have a larval stage restricted to the stream, and flying adults have the potential to leave the

confines of this specific dendritic spatial arrangement (Chaput-Bardy et al. 2009). The extent of overland and out-of-network movement is poorly understood (Hughes et al. 2009), as is the influence of water flow direction on larval movement within the channel (Lutscher et al. 2007). Dispersal in streams contributes to local population persistence and is demographically important (Speirs and Gurney 2001, Anderson et al. 2006, Lowe et al. 2006), so better understanding of these processes will enhance management of stream systems.

In this chapter, I review, summarise and illustrate some approaches to understanding invertebrate community assembly processes in dendritic networks, by synthesising analyses from my empirical tests in stream network invertebrate communities from preceding chapters and existing literature. I investigate community processes in dendritic networks at different spatial scales to understand network communities, dynamics and controls and thus review understanding of community assembly in dendritic networks and its applications. I frame my evaluation around three topics. Firstly, I discuss spatial distance measures in streams and some spatial statistical methods including interpretations of deterministic and stochastic community assembly processes. Secondly, I consider whether communities in networks function as metacommunities, and specifically consider the importance of habitat size and isolation to community assembly processes. Thirdly, I discuss the implications for restoration, management, sampling in network systems and ecological theory. My review shows that using an explicitly spatial approach to investigate communities, we can gain knowledge of important spatial processes that structure communities which are not currently well understood because of the limitations of traditional non-spatial methods.

1. Functional distance measures and statistical approaches for stream networks

Precise spatial analytical tools are needed to improve the effectiveness of spatial pattern analyses (McIntire and Fajardo 2009), particularly in streams. Spatial analyses such as those to detect the importance of multiple movement pathways of stream invertebrates, need appropriate spatial measures between interacting communities (Chapter 1). Appropriate spatial measures could be functional distance measurements, where the processes such as directionality and barriers to dispersal are taken into account to provide more realistic distances relating to organism movement (Chapter 1). Testing the fit of these functional distance measures to community data can help uncover mechanisms of movement (McIntire and Fajardo 2009), where different modes of dispersal can be inferred from the relative model fits and can be used to answer specific research questions. I found that the physical distance between communities measured along a stream network correlated with community patterns best, indicating that the majority of movement of these organisms was likely to be restricted to movement along the network rather than over land. Eigenvector methods, such as those used in Chapter one, can be analysed at various spatial scales (e.g. Laliberté et al. 2009), and extra details such as directional weighting components can be added to help understand more specific movement mechanisms (Blanchet et al. 2008b, Chapter 1). More detailed spatial distance metrics provided evidence for mechanisms of movement at smaller spatial scales, whereas processes such as overland flight acted at larger spatial scales, and could be inferred by the importance of Euclidean distance or measures of distance along stream networks (Chapter 1).

The need for appropriate methods for investigating spatial patterns and processes in streams will increase as awareness of the importance of spa-

tial relationships increases. The presence of spatial autocorrelation in data (non-independent errors), violates traditional statistical assumptions of independence (Ganio et al. 2005), and alternative statistical methods have been developed to circumvent this problem. For example, semivariograms, correlograms and Mantel tests have been used to investigate spatial patterns in streams (Ganio et al. 2005, Thompson and Townsend 2006, Heino et al. 2010). However, the use of spatial statistical analyses also depends on assumptions of the analyses. A key assumption in geostatistical methods is 'stationarity', i.e. the "correlation structure between neighbouring response values depends only on the distance between locations, not on their particular locations" (Ganio et al. 2005). Using spatial statistical approaches with the assumption of 'stationarity' to investigate spatial autocorrelation in streams could be inappropriate if we expect different processes to be acting in different parts of a stream network. Changing water velocity with distance downstream can influence drift rates and distances drifted by benthic invertebrates (Lutscher et al. 2007), so could be an example of a processes acting differently at various locations throughout a stream network. The effect of water velocity on movement will affect levels of connectance between communities in different parts of a stream network, suggesting that autocorrelation structure will not only rely on distance between sites, but also their positions in the network.

In addition to the differing influences of factors such as water velocity in different parts of stream networks, I showed that variability in community structure differs within the stream network, typically increasing with decreasing stream size (Chapter 4). In most standard spatial statistical analyses, equivalent distance measures are used to represent spatial structure between all pairs of locations. However, many distances could be *functionally*, quite different from each other (Grant et al. 2007, Peterson

et al. 2007). For example, overland or up- or down-stream distances may not be "perceived" to be equivalent by organisms and this would vary with their dispersal abilities. In streams, or indeed any network showing changes in connectivity between habitats, the statistical assumptions of stationarity may be invalid. Therefore, traditional geostatistical methods need to be adjusted to be appropriately applied to systems such as stream networks.

Examples of non-stationarity in streams, other than those demonstrated in chapter four, include responses to climate change, which depend on location within the network. In a study of stream fish assemblages in France, up-stream communities were found to become more dissimilar in their species composition, while down stream communities were found to become more similar to each other (Buisson and Grenouillet 2009). Brown and Swan (2010) also found that small headwater streams differed from larger mainstem reaches in community assembly processes. Ignoring such patterns could lead to incomplete or incorrect conclusions, and results from such spatial autocorrelation approaches need to be interpreted with caution. I encourage adaptation of existing spatial statistical approaches, such as weighting distances, using different distance measures and taking account of directionality when investigating spatial patterns and processes in stream networks (e.g. Chapter 1). These adaptations will increase the usefulness of spatial statistical approaches to a wider range of systems such as dendritic networks.

1.1. Deterministically controlled stochastic processes

Using various spatial statistical approaches, the detected spatial pattern in neutrally structured communities is often said to result from stochastic colonisation and extinction processes where communities are assembled by dispersal (Hubbell 2005, Chase 2007, Table 1). However, this

Table 1. A quick reference guide to some of the main metacommunity theories and mechanisms relating to spatial dynamics in stream networks.

Metacommunity theory term	**Explanation**	**References**
Mass effect (rescue effect)	Net flow of individuals created by differences in populations size of different patches influencing local community structure.	Holyoak et al. (2005)
Neutral perspective	Dynamics of species diversity are derived from probabilities of species loss (extinction, emigration) and gain (immigration, speciation).	Holyoak et al. (2005)
Niche perspective	Local abiotic conditions and/or differences in species life history traits determine community composition.	Holyoak et al. (2005)
Source-sink	Immigration into sink localities enhances local populations. Source patches produce a net excess of individuals that migrate to sink patches (where populations would decline to extinction without immigration from sources)	Holyoak et al. (2005)
Island biogeography theory (IBT)	The roles of extinction and colonisation are prominent in setting levels of biodiversity on habitat islands. The number of species present is a function of habitat patch size and distance from mainland population(s).	Holyoak et al. (2005)

spatial pattern may be present because of predicable "distance decays" (i.e. decreases in community similarity with increased spatial distance between communities), which are also associated with neutrally structured communities (Tuomisto and Ruokolainen 2008). Thus, the distance decay patterns within communities could be driven by stochastic population processes acting on species, but within a deterministic, spatial structure, like a stream network. Thereby spatially structured communities would result from this interaction between deterministic and stochastic factors (Chapter 2, Figure 2). More specifically, it could be that in streams, the physical network structure is a driver of dispersal limitation that makes stochastic colonisation and extinction (neutral) processes more important than for example, local habitat (niche) processes, for structuring communities (Fagan 2002, Labonne et al. 2008, Chapter 2). This means that network structure not only influences dispersal processes, but also the importance of dispersal processes in structuring the spatial component of communities (Figure 2).

Detection of spatial structure in communities in such a scenario needs to be interpreted using both stochastic and deterministic spatial structuring processes rather than just simple stochastic processes of colonisation and extinction. In stream networks for example, hydrology, geomorphology and disturbance are key network scale structuring forces determining community patterns in space (e.g. Chapter 3, Benda et al. 2004). The geomorphologically determined dendritic structure of stream networks appears to create specific dispersal pathways and / or habitat patterns that promote consistent spatial structure (Chapter 2). In addition, limitations on dispersal, induced by this specific spatial structure (Fagan 2002, Labonne et al. 2008), encourage stochastic processes to control the species composition over time (Chapter 2).

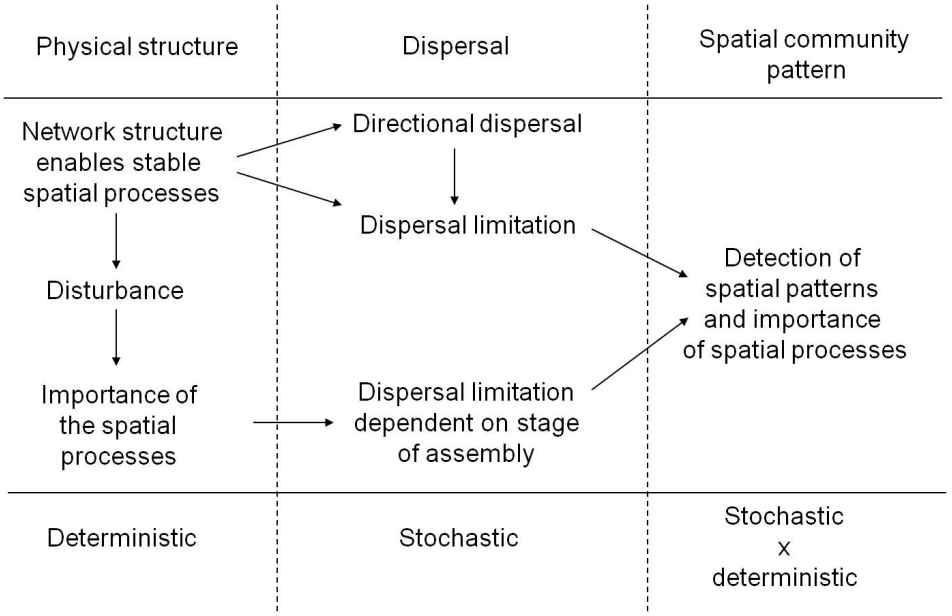

Figure 2. The influence of network structure via controls on dispersal limitation could be a key structuring mechanism for communities in dendritic networks. The imposed network structure is further enhanced by directional processes (flow) and frequent disturbance influencing the importance of colonisation and organism redistribution in a spatially explicit way. Thus, the effects of network structure conducted through dispersal limitation, disturbance and directionality influence the importance and detection of spatial processes in stream communities. This results in a combination of both deterministic and stochastic processes influencing the spatial pattern of local communities.

1.2. Spatially embedded environments: approaches for partitioning and shared variance

In the landscape view of stream networks where network structure has a profound influence on processes in streams (Fausch et al. 2002, Grant et al. 2007), methods used to separate the relative importance of niche and neutral assembly processes (Table 1) such as variance partitioning (Legendre et al. 2005) become confounded. These variance partitioning approaches used in other ecosystems are beginning to be critiqued in more detail (Smith and Lundholm 2010), but have received limited attention from stream ecologists. For example, the variance 'shared' by both spatial and environmental determinants (which cannot be separated statistically), is recognised as being

just as important as separate 'niche' and 'neutral' components (Smith and Lundholm 2010). The variance component shared by environmental and spatial variables is often large (e.g. Nabout et al. 2009, Chapter 3). Due to hierarchical, dendritic network relationships, streams provide an exaggerated example of environmental spatial patterning embedded in a spatial structure, making it particularly difficult to determine causal relationships between communities, environments and spatial processes. Instead of splitting variance components, my use of quantile regression showed that interactions between spatial and environmental community structuring processes limited variation in community composition (Chapter 4). Local communities are therefore controlled to various degrees by both environmental and spatial factors, each factor being potentially more limiting at various values of other limiting factors. For example, with some environmental characteristics, spatial processes become more or less limiting. Alternatively, given a particular dispersal limitation or probability, environmental factors could become more limiting. For example, environmental factors do not affect a species if it cannot get there (via spatial dispersal processes) in the first place. In communities that are not at the limits of environmental or spatial conditions, other limiting factors create variation in the community structure detected. Therefore, in all ecosystems, and particularly stream networks, I encourage alternative approaches in addition to variance partitioning to investigate details about the shared impacts of environmental and spatial processes, which are intrinsically linked. I have shown that quantile regression is effective for investigating joint limiting factors, while also indicating the presence of other contributing predictor variables, thus potentially providing more mechanistic detail than approaches resulting in high 'shared' variance partitions.

2. Metacommunity and island biogeography theories in dendritic networks

Several features that metacommunity and island biogeography theories have in common, and which are key to understanding community assembly processes, are considerations of connectance, isolation, habitat size and distances between communities (Holyoak et al. 2005, Kadmon and Allouche 2007, Table 1). A framework that combines these factors will help address the intertwined hierarchical nature of community structuring processes (Figure 3). I have developed a framework that combines processes at various spatial scales where components of neighbourhood configuration, local habitat size and local habitat conditions vary in importance depending on 'metacommunity' or 'network' scale factors (e.g. topology, disturbance, Figure 3). Overarching, but not explicitly measured in my research, is the influence of network structure on the actual dispersal of the organisms studied. Stream ecologists have tried to measure dispersal directly (e.g. with isotopes, directional trapping; Miller et al. 2002, Macneale et al. 2004), with variable success. Whereas my approach allows inferences to be made about dispersal processes at large scales to be made without direct measurement of organism movement, providing a more logistically reasonable approach. For example, for poorer dispersers (Figure 3b), particularly those whose movement is restricted to the network, topology or network configuration should become increasingly important for community assembly processes (Grant et al. 2007); local habitat factors remain important, but are not limiting (e.g. Chapter 4). On the other hand, for good dispersers (Figure 3a), spatial pattern determined by network shape should not be limiting if dispersal is widespread. However, for good dispersers, dispersal will still influence community processes, as organisms still need to move between

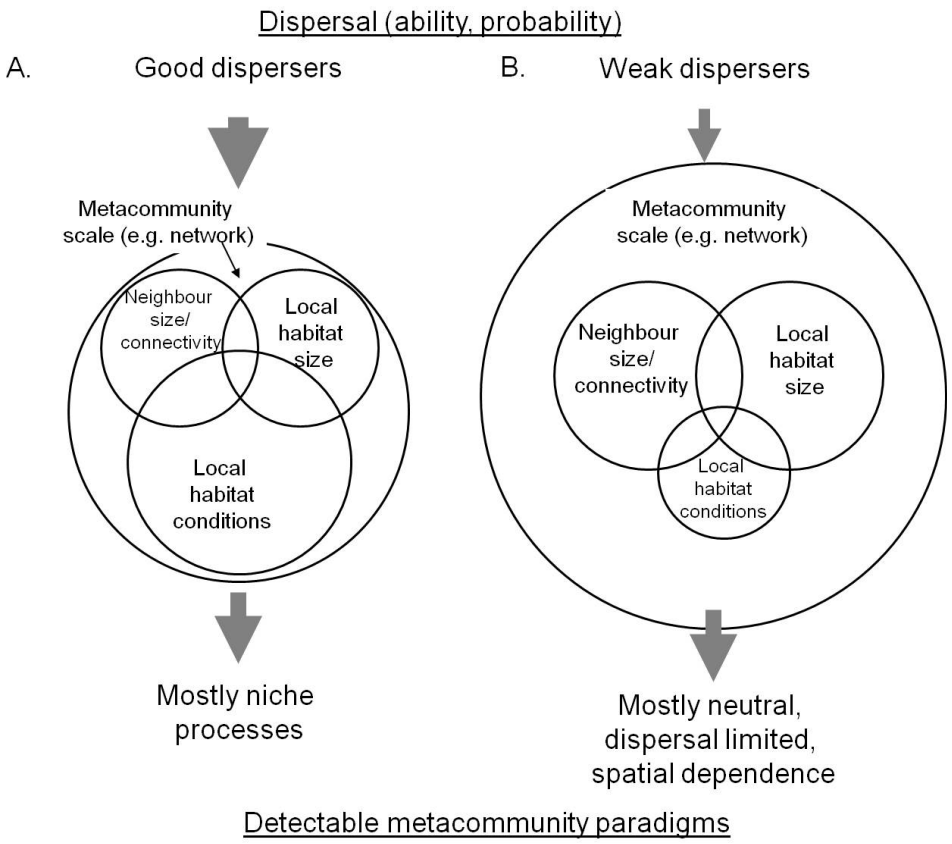

Figure 3. Key considerations defining the metacommunity processes detected across a metacommunity gradient. Connectance, habitat size, distance between communities and local habitat conditions are all influenced by network scale factors (e.g. topology, disturbance). Dispersal traits would further influence the relative importance of these combined factors structuring communities in dendritic networks. The combination of dispersal, network scale factors and local habitat conditions, local habitat size and neighbour size (all affected by network scale factors) results in different metacommunity processes being important for community structure. For example, species with good dispersal ability (A) should be more influenced by local habitat conditions than habitat size or neighbouring communities within the network, thus resulting primarily in niche processes controlling community assembly. On the other hand, weak dispersers (B) will be more affected by habitat size and the network neighbourhood, resulting in the importance of neutral and spatial processes controlling community assembly.

habitats. Thus, for widespread dispersers, local habitat and / or species interactions should have a greater influence on community composition than spatial factors.

2.1. At the network scale

At the network or metacommunity scale (outer circle, Figure 3), network topology and disturbance influence and encompass local scale factors. Processes at a network scale influence the metacommunity as a whole (Chapter 3). For example, disturbance will be propagated through the network depending on its branching (Benda et al. 2004, Grant et al. 2007), and some parts of networks will be consistently more likely to act as refugia for different organisms (Benda et al. 2004). Recovery from disturbance and the process of community assembly will therefore follow similar spatial patterns over time where organisms are redistributed or recolonise from spatial refugia and by drift in a spatially consistent manner (Chapter 2, Chapter 3). Therefore, network topology influences community assembly at the 'network' or 'metacommunity' scale, through these redistribution and colonisation processes. This is in addition to effects on the community of local habitat size distribution and extent of isolation, factors which are also influenced by the dendritic nature of the network.

2.2. Within network scale

Although the network or metacommunity scale can shed light on the mechanisms that assemble communities within networks, more detailed processes are involved at smaller scales within metacommunities. For example, the particular arrangement of habitats within a network, such as local and neighbourhood habitat size, should influence communities (Figure 3). However, very little empirical research has focussed on such issues.

Some studies have partially addressed habitat size and directional isolation by separating first and second order streams for analyses (e.g. Brown and Swan 2010). However, this split can be misleading, particularly under some branching patterns, for example, networks with side branching architecture where lower order branches link directly to the main-stem (Grant et al. 2007, Chapter 4). It is therefore important to go a step further and consider neighbourhood and adjacency effects in conjunction with other measures of isolation and habitat size (e.g. Chapter 4), rather than relatively coarse first and second order stream categories.

In support of island biogeography theory in which isolation, local habitat size and distance between communities are important for integrating metacommunity processes (Table 1), I address habitat size and adjacency effects on community processes at the within network scale (Figure 4, Chapter 4).

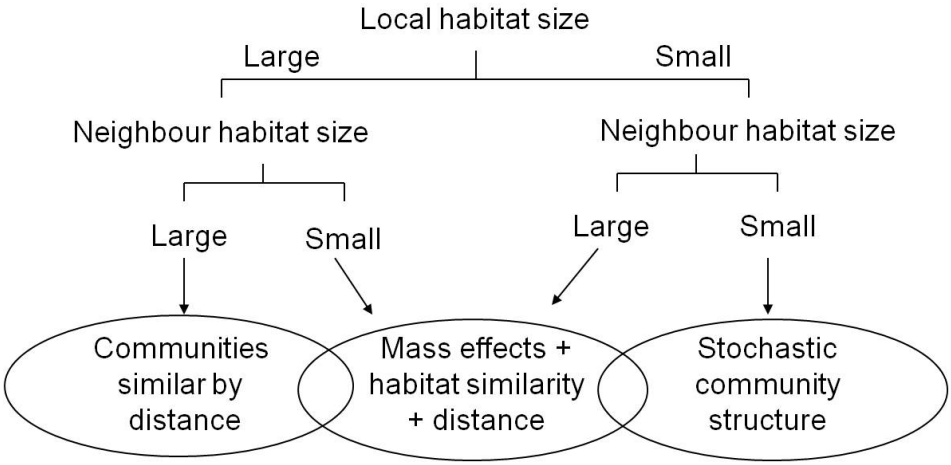

Figure 4. Island biogeography theory, metacommunity theory and spatial autocorrelation are combined (lower ovals) by considering local habitat size, isolation and neighbourhood effects on communities. Whether the local habitat size is 'large' or 'small', in combination with whether the neighbouring habitat size is 'large' or 'small' indicates which community structuring processes should be dominant. How similar communities within networks are to each other can be used to infer community interactions and metacommunity processes. Although I have characterised 'size' dichotomously, the transition between metacommunity processes is a continuous gradient, as indicated by the overlapping ovals.

Metacommunity processes such as 'Mass-effects' (Table 1), whereby larger habitats have more influence on nearby communities than smaller ones, will depend on these adjacency effects (Figure 4). Neighbourhood influences of this type have not been considered before in dendritic networks but are likely to be particularly important, so there is considerable further scope for research. For example, although I explicitly considered isolation, it can be complicated by stream flow and the nature of connected habitat 'patches'. Hence, habitat *length* may be important, particularly for fish (Coté et al. 2009), and processes such as water quality can have cumulative effects (Finlay et al. in press). Even with the simple measures of isolation I used in Chapter four, isolation was found to be important for structuring invertebrate communities in streams. With more information on the importance of various movement pathways (e.g. out of network vs. within network, movement distances) and direction, isolation could prove to be even more important for structuring communities in stream networks. Stream ecologists have long suspected the importance of dispersal, but have lacked techniques to investigate it at large scales. Considering aspects of metacommunity and island biogeography theory using spatially explicit analyses, I have shown that isolation, and by inference dispersal movement, is important in spatially structuring stream invertebrate communities.

3. Restoration, management and sampling to encompass network scale processes

Previous work at the network scale in streams has been limited (Grant et al. 2007, Clarke et al. 2008), but research at this scale may provide a missing link for explaining variability in stream community restoration success (Palmer 2009). Restoring or recovering ecological communities requires colonisation of restored habitat by organisms. Therefore knowledge of

dispersal processes including those between local communities (within metacommunities), could be useful for successful recovery of such ecosystems at large spatial scales. Because humans alter land cover, fragment stream networks through flow extraction leading to drying (Boulton 2003), and construct barriers to dispersal, such as dams and culverts (Schick and Lindley 2007, Coté et al. 2009), a multi-scale approach incorporating spatial network configuration is likely to be crucial for successful conservation and management of stream systems and the resources they provide (Lowe et al. 2006). Conservation and management of flow-connected, spatially complex systems requires consideration of spatial factors to ensure optimal and efficient use of resources and funding. Previous studies have shown that some features of landscape geometry (e.g. habitat size and connectivity) within the surrounding region can have significant effects on the resilience of communities to disturbance (Starzomski and Srivastava 2007). Therefore, restoring the spatial arrangement of the habitat, for example incorporating headwater and downstream habitats, may be crucial for maintaining processes such as dispersal, and ultimately the resilience of stream communities to perturbations. My results have the potential to aid conservation and management in streams by increasing understanding of the nature of spatial interactions and therefore the implications of human perturbations, and recovery from them, across multiple spatial scales.

3.1. Optimising restoration of riparian and catchment vegetation

Much stream restoration is based around mitigating deleterious land use effects on streams; for example, re-vegetating adjacent and surrounding land, or adding in-stream habitat (Palmer 2009). Recently, Death and Collier (2010) suggested that if 40-60% of a catchment was vegetated in forest or scrub, then 80% of stream invertebrate biodiversity could be

retained. Following on from this, it will be most useful to know *where* in a stream network vegetation cover will be most effective (e.g. Eikaas et al. 2005). Death and Collier (2010) assumed that it would be most important in 'headwater' catchments, but evidence that invertebrate communities have short recovery distances where streams flow from pasture into forest suggest this could be an over-simplification (Storey and Cowley 1997, Scarsbrook and Halliday 1999, Death and Collier 2010). Furthermore, communities in forest can potentially provide colonists in both up- and down-stream directions, increasing the viability of metacommunities in streams via either headwaters or main stems under forest cover (Chapter 4, Figure 5, Table 1). My research was undertaken on forested streams to identify spatial rather than land use effects, but it would be interesting and relevant to test where optimal locations occur, perhaps by undertaking targeted restoration trials in various parts of stream networks. Plans for prioritising revegetation, riparian management, and in-stream habitat restoration could include detecting the most 'influential' locations of communities within a network that will not only enhance the local restored community, but the whole network metacommunity (Figure 5). Therefore, targeting specific parts of networks could provide a way to use resources optimally for systematic conservation planning and reserve design (Clarke et al. 2008).

When considering source-sink metacommunity dynamics in dendritic networks, one needs to recognise that despite a predominance of down-stream flow-mediated processes, sources are not necessarily restricted to headwaters. Small headwater streams tend to be affected by more stochastic community processes (Chapter 4), which could mean that if the focus is to protect them (Freeman et al. 2007, Wipfli et al. 2007, Clarke et al. 2008), there maybe a greater likelihood of extinctions for some species. Although headwaters generally have high beta diversity (Clarke et al. 2008), the in-

creased risk of extinction suggests a need to assess the relative importance of larger down stream reaches and small headwater streams to stream meta-community viability at the network scale. There are also different human demands on larger downstream reaches of streams (e.g. water extraction), which decrease habitat size and may affect the sustainability of communities within the entire network.

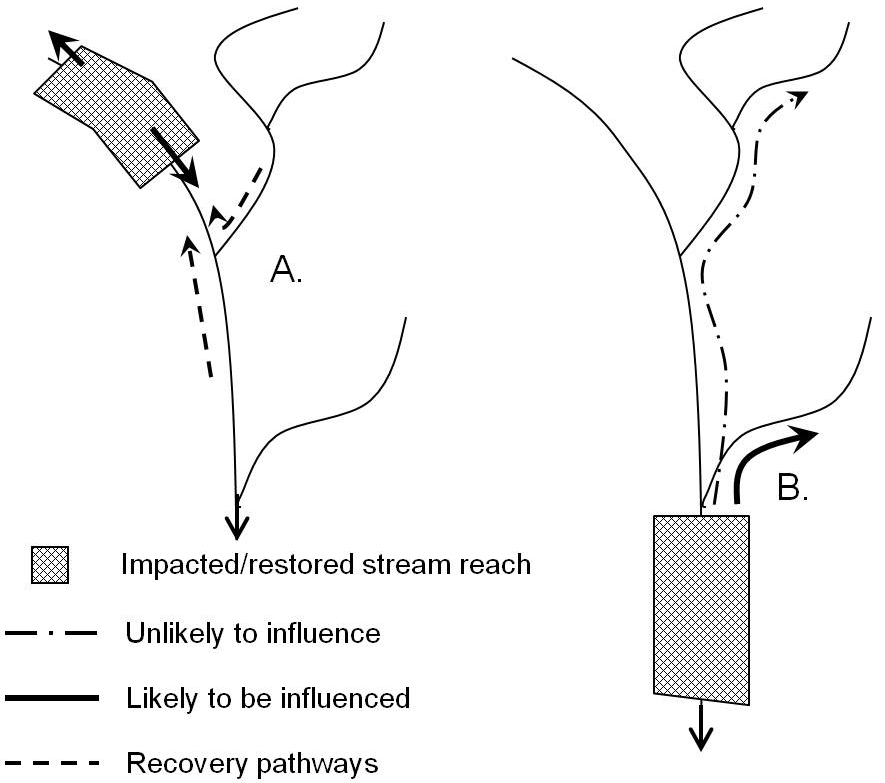

Figure 5. In restoration / rehabilitation most previous studies have assumed or suggested headwater stream reaches as 'sources' for colonists and resources due to the directional flow of streams. Upstream reaches can influence downstream reaches, but recovery of communities as they enter forested reaches down stream can also be over short distances, suggesting the downstream flow effect may not be overly influential (A). The opposite possibility is that larger downstream reaches act as 'sources' (B). Which parts of streams can act as 'sources' has implications for both degradation in different parts of stream networks and for optimal riparian vegetation restoration. My research indicates the influence of a degraded or restored site on other parts of a stream network will depend primarily on the size of the impacted / restored site and its relative location in the network (e.g. central or isolated).

In addition to the consideration of the relative importance of parts (e.g. Headwaters, main stems) of streams, processes within streams such as disturbance may also influence the importance of spatial connectance. Restoring local habitat in stream networks that are naturally disturbed, may not be as efficient for maintaining or enhancing biodiversity as in less disturbed streams. For example, I showed in Chapter three that spatial processes were more important for structuring communities than local niche conditions in more flood disturbed stream networks. To facilitate redistribution and recolonisation of organisms within a network, the maintenance of high connectance between sites may be more important in some situations for sustaining network metacommunities than in-stream habitat improvement alone. Therefore, to maintain functioning metacommunities we need to consider more than the traditional restoration philosophy of 'build it and they will come' (Bond and Lake 2003), by being aware of the sources of individuals and the pathways for processes such as dispersal.

3.2. Spatially representative sampling and monitoring

If different processes occur in different parts of networks (Chapter 4), sampling in an opportunistic manner (e.g. at the most accessible points on a stream) could be potentially misleading and mask the patterns one wants to detect (Dobbie et al. 2008). No processes that I know of are directly comparable at various scales and parts of streams, but generally this subject is poorly understood. My results suggest that sites central to the network (well connected, close to junctions, relatively large size) may be most representative and influential on the surrounding communities, whereas, small streams are unlikely to reveal much in terms of predictability of communities in other parts of the network (Chapter 4). My networks are however small headwater networks and other measures of centrality may

be necessary for other types of river networks. Although small streams are likely to have more random communities in the sense of 'representativeness', they provide other important sources of diversity such as high beta-diversity (Clarke et al. 2008). Based on my results, it does matter where you sample or monitor streams if you are intending to compare them to each other, treat them as replicates or capture spatial pattern (Dobbie et al. 2008). Not only should samples, for example, those for environmental monitoring, be taken from a similar position in a network, but consideration of their 'centrality' and therefore how representative they are of the network metacommunity is needed.

Lastly, my sampling of adult caddisflies resulted in generally similar conclusions about spatial processes in stream network invertebrate communities as sampling benthic larval communities (Chapter 4). As the identification, processing and sampling of adults can sometimes be easier than for benthic communities, their use should be encouraged in studies of spatial processes and patterns. Sampling both larval and adult life stages can also add information on life histories and spatial patterns of communities, and therefore increase understanding of community structuring mechanisms (Chapter 4, Miller et al. 2002, Smith et al. 2009). When sampling or monitoring for recovery in streams, it may therefore be useful to consider the multiple movement and recovery pathways such as those of multiple life stages and their relative importance for ecosystem recovery.

Summing up: implications for ecological theory and management

I have shown that the spatial arrangement and dendritic geometry of stream networks can partly control aquatic invertebrate community assembly processes. Consideration of these spatial influences and processes has led

to new insights in population and community ecology in stream networks and other dendritic systems (Grant et al. 2007). The results can also shed light on useful guidelines for research, improved management, restoration and the design of potential reserves within dendritic networks.

Habitat conditions and spatial processes are intrinsically linked in stream communities because of their hierarchical, dendritic network structure. As I have indicated, knowledge of the interactions between spatial structure and habitat characteristics are important for a better understanding of spatial, stochastic and deterministic processes. Although spatial structure is generally attributed to stochastic processes, they can in turn be structured by deterministic processes that result in consistent dispersal pathways, while maintaining the elements of 'chance' inherent in species colonisation and extinction.

The various ways to consider spatial arrangement on dispersal limitation and metacommunity processes discussed in this thesis highlight the potential these developments have, and their versatility for guiding wider aspects of ecology and ecological theory. Although stream networks are complex systems to understand, it is promising that logical theoretical hypotheses such as those based on island biogeography theory, are supported. Not all parts of streams are created equal and further understanding of the importance of community structuring processes can be gained by expanding on the kinds of research into spatial aspects such as habitat size, connectivity and directional processes in dendritic networks reported in this thesis.

"The more comfortable we become with being stupid, the deeper we will wade into the unknown and the more likely we are to make big discoveries."

-- Martin A. Schwartz

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Appendix A. Presence (1), absence (0), and total richness of macroinvertebrate taxa in each of the stream networks sampled in January or February 2008 (time 1) and November or December 2008 (time 2). Time 1 was used in Chapter 1 and Chapter 4.

			Network							
			Foley Creek		Ongionui Stream		Coal Creek		Maori Gully Stream	
		Species	Time 1	Time 2	Time 1	Time 2	Time 1	Time 2	Time 1	Time 2
Trichoptera	Hydropsychidae	Hydropsychidae sp.	0	0	0	0	0	0	1	1
		Aoteapsyche sp.	1	1	1	1	1	0	1	0
	Hydroptilidae	*Oxyethira albiceps*	1	1	1	1	1	1	1	1
		Paroxyethira sp.	1	0	0	0	0	0	0	0
	Hydrobiosidae	Hydrobiosidae sp.	0	1	1	1	1	1	1	0
		Psilochorema sp.	0	1	1	1	1	1	1	1
		Hydrobiosis clavigera	0	0	0	0	0	0	1	0
		Hydrobiosis copis	0	0	0	0	0	0	1	0
		Hydrobiosis frater	0	0	0	1	0	0	0	0
		Hydrobiosis gollanis	0	0	1	1	1	0	1	1
		Hydrobiosis parumbripennis	1	0	0	0	0	0	1	1
		Hydrobiosis umbripennis	0	0	0	0	0	0	1	1
		Hydrobiosis spatulata	0	0	0	0	0	0	0	1
		Tiphobiosis sp.	0	0	0	0	0	1	1	1
		Traillochorema sp.	0	0	0	1	0	0	0	0
		Costachorema sp.	0	1	0	0	0	1	1	1
	Polycentropodidae	*Polyplectropus* sp.	0	0	0	1	1	1	1	1

Appendix A (continued)

		Network							
		Foley Creek		Ongionui Stream		Coal Creek		Maori Gully Stream	
	Species	Time 1	Time 2	Time 1	Time 2	Time 1	Time 2	Time 1	Time 2
	Plectrocnemia maclachlani	0	0	1	1	1	0	1	1
Philopotamidae	*Hydrobiosella* sp.	0	1	0	1	1	1	1	1
Helicopsychidae	*Rakiura* sp.	0	1	0	0	1	1	0	0
	Helicopsyche sp.	1	1	1	1	1	1	1	1
Oeconesidae	*Oeconesus* sp.	0	0	1	1	0	0	1	1
	Pseudoeconesus sp.	0	0	0	1	0	0	1	1
Leptoceridae	*Hudsonema alienum*	1	0	1	0	1	0	1	0
	Hudsonema amabile	1	0	1	1	0	0	0	0
	Triplectides sp.	0	0	1	1	1	1	0	1
	Triplectidina sp.	0	0	0	1	0	0	0	0
Philorheithridae	*Philorheithrus* sp.	0	0	1	1	0	0	0	0
Calocidae	*Pycnocentrella eruensis*	1	1	1	0	1	0	0	1
Helicophidae	*Zelolessica cheira*	0	1	1	1	1	1	1	1
	Alloecentrella magnicornis	0	0	1	1	1	1	0	1
Conoesucidae	*Pycnocentrodes* sp.	0	0	0	1	0	0	1	0
	Beraeoptera sp.	0	0	0	0	1	1	0	0
	Pycnocentria evecta	0	0	1	1	1	1	0	0
	Pycnocentria forcipata	0	0	1	1	0	1	0	0
	Pycnocentria gunni	0	0	0	0	1	1	0	1

Appendix A (continued)			Network							
			Foley Creek		Ongionui Stream		Coal Creek		Maori Gully Stream	
		Species	Time 1	Time 2	Time 1	Time 2	Time 1	Time 2	Time 1	Time 2
		Pycnocentria hawdonia	0	0	0	0	0	0	1	0
		Pycnocentria sylvestris	0	0	1	0	1	1	0	0
		Pycnocentria sp.	0	1	0	1	0	1	1	0
		Olinga feredayi	1	0	1	1	1	1	0	1
Trichoptera species richness			9	11	19	24	20	19	23	21
Ephemeroptera	Leptophlebiidae	*Deleatidium* sp.	1	1	1	1	1	1	1	1
		Mauiulus luma	0	0	0	1	0	0	0	1
		Zephlebia sp.	0	1	1	1	1	1	0	1
		Neozephlebia scita	0	1	0	1	1	1	0	1
		Atalophlebioides cromwelli	0	0	1	1	0	1	0	0
		Austroclima sp.	0	0	1	1	1	0	0	1
	Ephemeridae	*Ichthybotus bicolor*	0	1	0	0	0	0	0	0
	Coloburiscidae	*Coloburiscus humeralis*	1	1	1	1	1	1	1	1
	Nesameletidae	*Nesameletus ornatus*	0	0	1	1	0	0	1	1
	Oniscigastridae	*Onicigaster wakefieldi*	0	0	0	1	0	0	0	1
	Ameletopsidae	*Ameletopsis perscitus*	0	1	1	1	1	1	1	1
Ephemeroptera species richness			2	6	7	0	6	6	4	9
Plecoptera	Eustheniidae	*Stenoperla* sp.	1	1	1	1	1	1	1	1
	Austroperlidae	*Austroperla cyrene*	1	1	1	1	1	1	1	1

Appendix A (continued)

			Network							
			Foley Creek		Ongionui Stream		Coal Creek		Maori Gully Stream	
		Species	Time 1	Time 2	Time 1	Time 2	Time 1	Time 2	Time 1	Time 2
	Gripopterygidae	*Megaleptoperla* sp.	0	0	1	1	0	1	0	1
		Acroperla sp.	0	0	0	1	0	0	0	0
		Nesoperla fulvescens	0	0	0	1	0	0	0	0
		Zelandoperla sp.	1	1	1	1	1	0	1	1
		Taraperla ancilis	1	1	1	1	1	1	1	1
	Antarctoperlinae	*Zelandobius* sp.	1	1	1	1	1	1	1	1
		Zelandobius illiesi	0	0	0	0	0	0	0	1
	Notonemouridae	*Spaniocercoides* sp.	1	1	1	1	1	1	1	1
		Cristaperla sp.	1	0	1	0	0	0	1	1
		Halticoperla sp.	1	0	0	0	0	0	0	0
		Spaniocerca sp.	0	1	1	1	1	1	1	1
Plecoptera species richness			8	7	9	10	7	7	8	10
Diptera	Tipulidae	*Limonia* sp.	0	1	0	1	1	0	1	0
		Aphrophila sp.	0	1	1	1	1	1	1	1
		Hexatomini	1	0	0	1	0	0	0	1
		Paralimnophila sp.	1	0	0	1	1	0	1	0
		Eriopterini	0	1	1	1	1	1	1	1
	Tanyderidae	*Mischoderus* sp.	0	0	0	1	0	0	0	0
	Dixidae	*Paradixa*	0	0	1	0	0	0	0	1

Appendix A (continued)

			Network							
			Foley Creek		Ongionui Stream		Coal Creek		Maori Gully Stream	
		Species	Time 1	Time 2	Time 1	Time 2	Time 1	Time 2	Time 1	Time 2
	Simuliidae	*Austrosimulium* sp.	1	1	1	1	1	1	1	1
	Chironomidae	Tanypodinae	0	1	1	1	1	1	1	1
		Chironomidae	1	1	1	1	1	1	1	1
	Ceratopogonidae	Ceratopogoninae	1	1	1	1	1	1	1	1
	Empididae	Empididae (Type A)	0	1	1	1	1	1	1	1
		Empididae (Type B)	1	0	0	0	0	0	0	0
	Muscidae	Muscidae	0	0	0	1	1	0	1	0
	Blephariceridae	Blephariceridae	0	1	0	0	0	1	0	0
	Stratiomyidae	Stratiomyidae	1	0	0	1	0	0	0	1
Diptera species richness			7	9	8	13	10	8	10	10
Coleoptera	Elmidae	Elmidae (adult)	1	0	1	0	1	0	0	0
		Hydora sp.	0	1	1	1	1	1	1	1
		Zeohydora sp.	0	1	1	1	1	1	0	1
	Hydraenidae	Hydraenidae (adult)	0	1	1	1	1	1	1	1
	Hydrophilidae	Hydrophilidae	0	0	1	1	1	0	1	1
	Ptilodactylidae	Ptilodactylidae	1	1	1	1	0	0	1	1
	Scirtidae	Scirtidae	1	1	1	1	0	0	1	0
Coleoptera species richness			3	5	7	6	5	3	5	5
Megaloptera		*Archichauliodes diversus*	1	1	1	1	1	1	1	1

Appendix A (continued)

		Network							
		Foley Creek		Ongionui Stream		Coal Creek		Maori Gully Stream	
	Species	Time 1	Time 2	Time 1	Time 2	Time 1	Time 2	Time 1	Time 2
Crustacea	Amphipoda	0	1	0	1	1	0	1	1
	Platyhelminthes	1	0	1	1	0	0	0	0
	Gastropoda	0	1	1	1	0	0	0	1

Appendix B

Appendix B. Forward selected spatial variables explaining significant variation ($\alpha < 0.1$) in community composition in four West Coast, South Island, stream networks. The R^2 was adjusted for multiple comparisons (R^2_a) which controls for variation in sample size. P is the probability value for the significance of the vector explaining variation in the invertebrate communities from forward selection. Eigenvalues represent the spatial scale of the explained variation. Negative eigenvalues represent negative spatial autocorrelation, and positive eigenvalues, positive spatial autocorrelation. The absolute magnitude of the eigenvalues indicates whether they explained large or small scale spatial variation in community composition. Distance metric acronyms are defined in Table 1 (Chapter 1).

	Distance Metric	**Vector number**	**R^2_a (cumulative)**	**P**	**Eigenvalue**
Foley Creek	EMEM	1	0.054	0.048	6181088
		2	0.112	0.037	3033054
		16	0.154	0.088	-4140559
		4	0.200	0.073	752304
	SMEM	2	0.116	0.001	6401096
		1	0.209	0.008	10247400
		14	0.258	0.042	-5475363
		5	0.312	0.032	925226
		16	0.347	0.091	-8174054
		6	0.387	0.080	-892464
		11	0.431	0.078	-2984642
		8	0.477	0.086	-2944573
		3	0.527	0.092	2891613
	AEM1	2	0.127	0.001	1058.3
		5	0.217	0.002	794.1
		4	0.279	0.013	806.1
		6	0.323	0.041	423.2
		7	0.371	0.056	386.5
		1	0.412	0.079	1870.5
		11	0.455	0.081	169.7
	AEM2	1	0.107	0.005	992.1
		5	0.204	0.003	262.9
		3	0.243	0.075	404.3
		8	0.284	0.074	148.3
	AEM3	5	0.086	0.009	99.4
		9	0.135	0.076	11.3
		1	0.189	0.063	644.9

Appendix B (continued)

	Distance Metric	Vector number	R^2_a (cumulative)	P	Eigenvalue
Coal Creek	EMEM	1	0.073	0.022	34775882
		9	0.133	0.045	-6805840
		2	0.190	0.038	7537525
	SMEM	1	0.068	0.026	46756330
	AEM1	1	0.106	0.003	2779.4
		7	0.175	0.022	290.0
		12	0.235	0.040	139.6
	AEM2	1	0.088	0.012	2149.2
		8	0.137	0.060	148.8
		13	0.188	0.096	76.2
		3	0.233	0.090	506.4
		9	0.284	0.078	111.2
	AEM3	1	0.079	0.022	52.6
		11	0.151	0.057	2.4
Ongionui Stream	EMEM	7	0.055	0.090	-260327
		8	0.118	0.071	-371295
	SMEM	8	0.173	0.002	-1313760
		3	0.219	0.058	845421
		6	0.260	0.084	-553065
	AEM1	2	0.137	0.012	691.7
		1	0.279	0.001	1174.5
	AEM2	5	0.129	0.004	144.4
		9	0.185	0.069	87.3
	AEM3	4	0.071	0.053	20.4
		1	0.153	0.030	176.2
		7	0.220	0.057	11.9
		2	0.287	0.069	49.2
		12	0.366	0.059	3.5
Maori Gully Stream	EMEM	1	0.072	0.029	2340923
		11	0.144	0.039	-514358
	SMEM	11	0.088	0.021	-922682
		4	0.183	0.008	800381
		1	0.274	0.001	4334191
		9	0.311	0.065	-880208
		3	0.351	0.059	1524562

Appendix B (continued)

Distance Metric	Vector number	R^2_a (cumulative)	P	Eigenvalue
AEM1	2	0.073	0.028	813.7
	1	0.128	0.054	1339.1
	6	0.183	0.068	359.1
	8	0.230	0.088	232.8
	14	0.277	0.087	94.7
AEM2	14	0.103	0.012	63.6
	1	0.188	0.009	832.2
	3	0.231	0.057	228.0
AEM3	16	0.096	0.015	2.5
	1	0.149	0.032	158.0
	2	0.208	0.038	89.2
	11	0.267	0.038	6.6
	18	0.322	0.027	0.4
	8	0.362	0.060	12.3
	17	0.399	0.092	0.5

Appendix C

Appendix C. Hydrological modelling parameters

Sub-basin components		**Derivation**
Area		From REC* or calculated using spatial analyst hydrology tools when not present in REC
Loss method		SCS Curve number
	Curve number	Estimated from Mays (2005) in conjunction with LRI*, LENZ* and LCDB*
Transform method		SCS unit hydrograph
	Lag time	Calculated from equation in Mays (2005)
Baseflow method		Constant monthly
	Baseflow	West Coast - Field discharge measurements. Otago – FWENZ* variable 'segflow'
Reach components		
Routing method		Muskingum-Cunge
	Length	From REC or calculated in GIS when stream networks did not match the REC
	Slope	FWENZ variable 'segslope' or calculated from the DEM*
	Manning's n	West Coast –estimated from Hicks and Mason (1991) and photos of the sites. Otago – estimated from $n = 0.015\ D_{50}^{1/6}$ where D_{50} is the median diameter of the bed surface material in mm (Harding et al. 2004)
	Bottom width	Measured in field
	Side slope	West Coast - estimated from site knowledge, field measurements and site photos. Otago from bankfull and stream width measurements.
Rainfall		CliFlo data – daily rainfall for one year up to each sampling date from the nearest weather station (http://cliflo.niwa.co.nz/).

* REC - River Environments Classification

FWENZ - Fresh water environments New Zealand

DEM - Digital Elevation Model

LRI - Land Resource inventory

LENZ - Land Environments New Zealand

LCDB2 - Land cover Database

Appendix D

Appendix D. Species list and dispersal traits.

Order	Family	Species	Dispersal ability (1 = high, 0 = low)	
			Larval or water	Adult flight
Trichoptera	Hydropsychidae	Hydropsychidae sp.	0	1
		Aoteapsyche sp.	0	1
		Diplectrona sp.	0	1
	Hydroptilidae	*Oxyethira albiceps*	0	1
		Paroxyethira sp.	0	1
	Hydrobiosidae	Hydrobiosidae sp.	0	1
		Psilochorema sp.	0	1
		Hydrobiosis clavigera	0	1
		Hydrobiosis copis	0	1
		Hydrobiosis gollanis	0	1
		Hydrobiosis parumbripennis	0	1
		Hydrobiosis umbripennis	0	1
		Costachorema sp.	0	1
		Hydrobiosis spatulata	0	1
		Tiphobiosis sp.	0	1
	Polycentropodidae	*Polyplectropus* sp.	0	1
		Plectrocnemia maclachlani	0	1
	Philopotamidae	*Hydrobiosella* sp.	0	1
	Helicopsychidae	*Rakiura* sp.	0	1
		Helicopsyche sp.	0	1
	Oeconesidae	*Oeconesus* sp.	0	1

Appendix D (continued)

Order	Family	Species	Dispersal ability (1 = high, 0 = low) Larval or water	Adult flight
		Pseudoeconesus sp.	0	1
	Leptoceridae	*Hudsonema alienum*	0	1
		Hudsonema amabile	0	1
		Triplectides sp.	0	1
		Oecetis sp.	0	1
	Philorheithridae	*Philorheithrus* sp.	0	1
	Calocidae	*Pycnocentrella eruensis*	0	1
	Helicophidae	*Zelolessica cheira*	0	1
		Aloecentrella magnicornis	0	1
	Conoesucidae	*Pycnocentrodes* sp.	0	1
		Beraeoptera sp.	0	1
		Pycnocentria evecta	0	1
		Pycnocentria forcipata	0	1
		Pycnocentria gunni	0	1
		Pycnocentria hawdonia	0	1
		Pycnocentria sylvestris	0	1
		Pycnocentria sp.	0	1
		Olinga feredayi	0	1
Ephemeroptera	Leptophlebiidae	*Deleatidium* sp.	1	0
	Ephemeridae	*Ichthybotus bicolor*	0	0
		Mauiulus luma	1	0

Appendix D (continued)			Dispersal ability (1 = high, 0 = low)	
Order	**Family**	**Species**	**Larval or water**	**Adult flight**
		Zephlebia sp.	1	0
		Neozephlebia scita	1	0
		Atalophlebioides cromwelli	1	0
		Austroclima sp.	1	0
	Coloburiscidae	*Coloburiscus humeralis*	1	0
	Nesameletidae	*Nesameletus ornatus*	1	0
	Oniscigastridae	*Onicigaster wakefieldi*	1	0
	Ameletopsidae	*Ameletopsis perscitus*	1	0
Plecoptera	Eustheniidae	*Stenoperla* sp.	0	1
	Austroperlidae	*Austroperla cyrene*	0	0
	Gripopterygidae	*Megaleptoperla* sp.	0	0
		Zelandoperla sp.	0	0
		Taraperla ancilis	0	0
	Antarctoperlinae	*Zelandobius illiesi*	0	0
		Zelandobius sp.	0	0
	Notonemouridae	*Spaniocercoides* sp.	1	0
		Cristaperla sp.	0	0
		Halticoperla sp.	0	0
		Spaniocerca sp.	1	0
Diptera	Tipulidae	*Limonia* sp.	0	0
		Aphrophila sp.	0	0

Appendix D (continued)

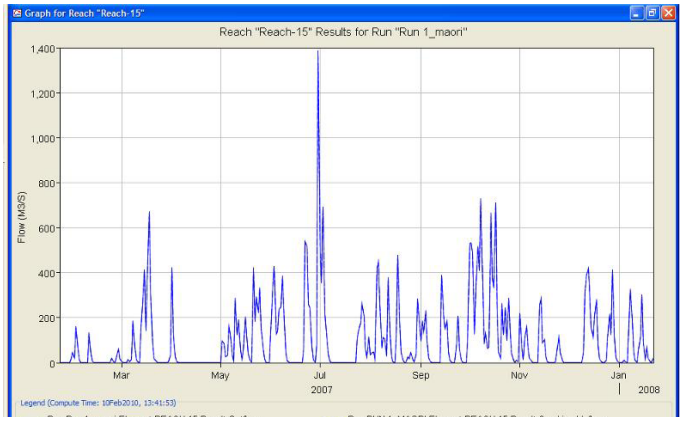
Order	Family	Species	Dispersal ability (1 = high, 0 = low) Larval or water	Adult flight
		Hexatomini	0	0
		Paralimnophila skusei	0	0
		Eriopterini	0	0
		Zelandotipula	0	0
	Tabanidae	Tabanid sp.	0	0
	Psychodidae	*Psychoda* sp.	0	0
	Dixidae	*Paradixa*	0	0
	Simuliidae	*Austrosimulium* sp.	0	1
	Tanyderidae	Tanyderidae	0	0
	Chironomidae	Tanypodinae	1	1
		Chironomidae	1	1
	Ceratopogonidae	Ceratopogoninae	0	0
	Empididae	Empididae (Type A)	0	0
		Empididae (Type B)	0	0
	Muscidae	Muscidae	0	1
	Blephariceridae	Blephariceridae	0	0
	Stratiomyidae	Stratiomyidae	0	0
Coleoptera	Elmidae	Elmidae (adult)	0	1
		Hydora sp.	0	0
		Zeohydora sp.	0	0
	Hydraenidae	Hydraenidae (adult)	1	1

Appendix D (continued)			Dispersal ability (1 = high, 0 = low)	
Order	**Family**	**Species**	**Larval or water**	**Adult flight**
	Hydrophilidae	Hydrophilidae	0	1
		Berosus sp.	0	1
	Ptilodactylidae	Ptilodactylidae	0	1
	Scirtidae	Scirtidae (A)	1	1
Megaloptera	Corydalidae	*Archichauliodes diversus*	0	0
Other		Amphipoda	0	0
		Platyhelminthes	0	0
		Gastropoda	0	0

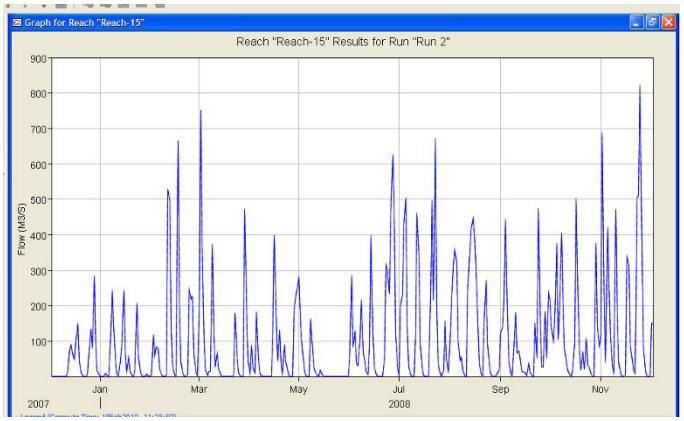
Appendix E

Appendix E. Hydrographs for each network calculated at the most down-stream sampling reach.

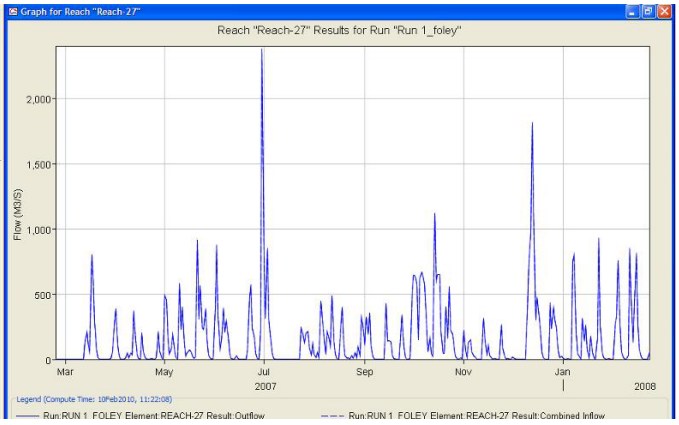
Maori Gully Stream, West Coast - time 1



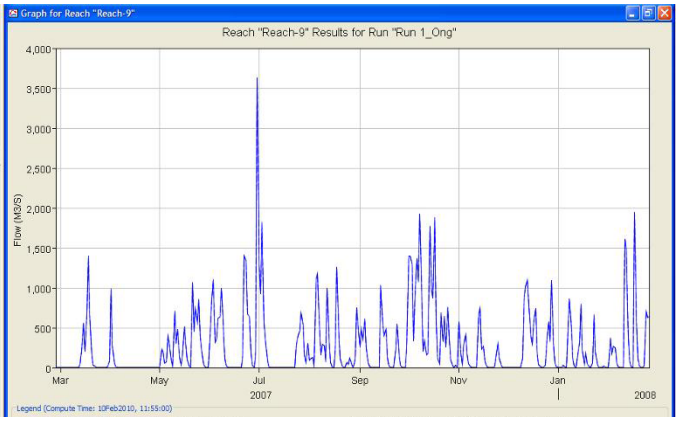
Maori Gully Stream, West Coast - time 2



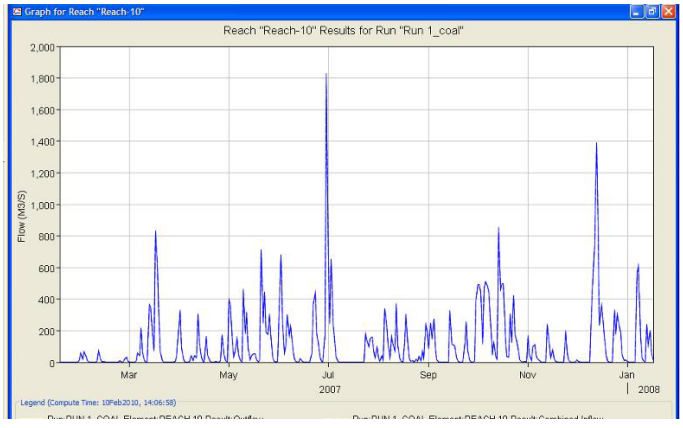
Foley Creek, West Coast - time 1



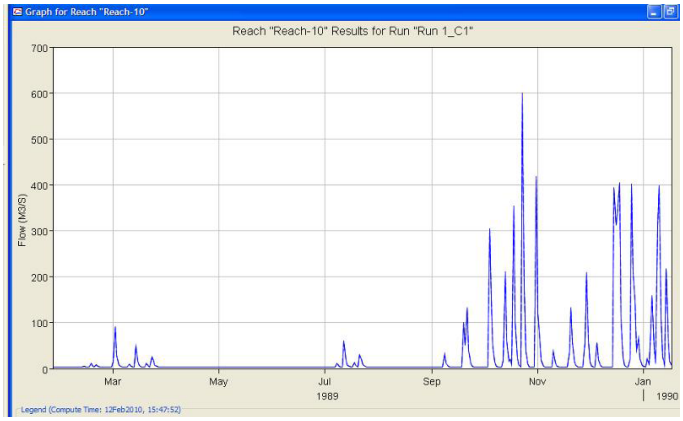
Ongionui Stream, West Coast - time 1



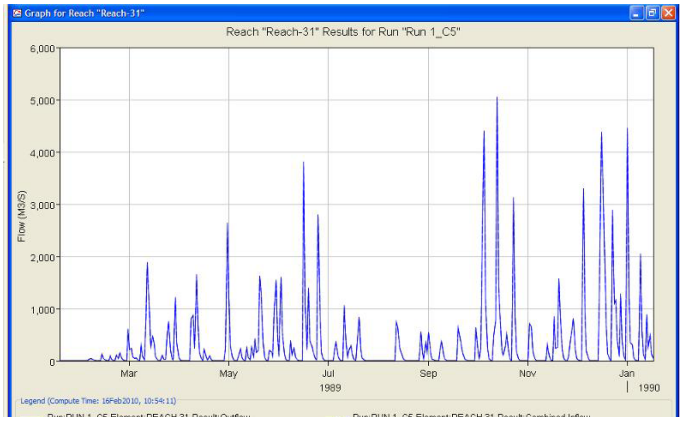
Coal Creek, West Coast - time 1



Shepherd Stream, Otago

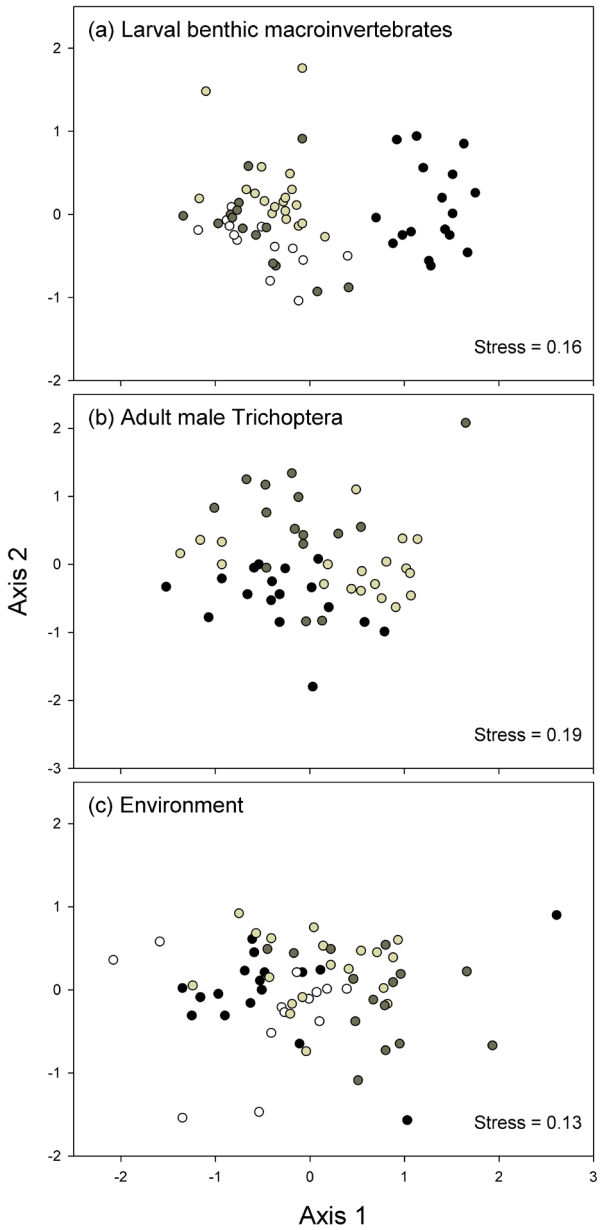


Silver Stream, Otago



Appendix F

Appendix F. Non-metric multidimensional scaling plots for (a) larval benthic macroinvertebrates, (b) adult male Trichoptera and (c) environmental variables. Shading represents the different stream networks where black = Foley Creek, dark grey = Coal Creek, light grey = Maori Gully Stream, white = Ongionui Stream (adults were not sampled at Ongionui Stream).



Appendix G

Appendix G. Species list of adult Trichoptera captured in light traps on the West Coast of the South Island New Zealand. Specimens of these species are held in a reference collection within the Freshwater Ecology Research Group at the University of Canterbury, New Zealand.

		Stream network		
Family	**Species**	**Maori Gully Stream**	**Foley Creek**	**Coal Creek**
Calocidae	*Pycnocentrella eruensis*	1	1	1
Conoesucidae	*Olinga feredayi*	1	1	1
	Pycnocentria evecta	1	1	1
	Pycnocentria gunni	0	0	1
	Pycnocentria sp. (undescribed)	0	1	1
	Pycnocentrodes aeris	0	1	0
	Pycnocentrodes aureola	1	1	1
Ecnomidae	*Ecnomina zealandica*	0	1	0
Helicopsychidae	*Helicopsyche albescens*	1	1	1
	Helicopsyche howesi	0	1	0
	Helicopsyche poutini	1	0	1
	Helicopsyche zealandica	0	0	1
	Rakiura vernale	1	0	0
Hydrobiosidae	*Costachorema* sp.	0	0	1
	Costachorema xanthoptera	0	1	0
	Edpercivalia fusca	0	1	1
	Edpercivalia maxima	0	1	1
	Edpercivalia sp.	1	1	0
	Edpercivalia spaini	0	1	1
	Hydrobiosis chalcodes	0	1	0
	Hydrobiosis copis	0	0	1

Appendix G (continued)		Stream network		
Family	**Species**	**Maori Gully Stream**	**Foley Creek**	**Coal Creek**
	Hydrobiosis gollanis	1	1	1
	Hydrobiosis parumbripennis	0	1	0
	Hydrobiosis silvicola	0	1	0
	Hydrobiosis soror	0	1	1
	Hydrobiosis umbripennis	0	1	0
	Hydrochorema sp.	0	0	1
	Hydrochorema tenuicaurdatum	0	1	0
	Neurochorema sp.	0	1	0
	Psilochorema bidens	0	1	0
	Psilochorema leptoharpax	0	1	1
	Psilochorema mimicum	0	1	0
	Psilochorema nemorale	0	1	0
	Psilochorema tautoru	1	1	1
	Psilochorema vomerharpax	0	0	1
	Tiphobiosis sp.	0	1	1
Hydropsychidae	*Aoteapsyche raruraru*	1	1	1
	Aoteapsyche tepoka	1	0	0
	Aotepsyche colonica	1	1	1
Hydroptilidae	Hydroptilidae	1	1	1
Kokiriidae	*Kokiria miharo*	0	0	1
Leptoceridae	*Hudsonema aliena*	1	1	0

Appendix G (continued)

Family	Species	Stream network		
		Maori Gully Stream	Foley Creek	Coal Creek
	Hudsonema amabile	0	1	0
	Triplectides cephalotes	0	1	0
	Triplectides dolichos	1	1	1
	Triplectidina oreolimnetes	1	1	1
Oeconesidae	*Oeconesus maori*	1	1	1
	Pseudoeconesus hudsoni	0	1	1
	Pseudoeconesus stramineus	1	1	1
Philopotamidae	*Hydrobiosella mixta*	1	1	0
	Hydrobiosella stenocerca	1	1	1
	Hydrobiosella tonela	0	1	0
	Philopotamidae sp.	0	1	1
Philorheithridae	*Philorheithrus agilis*	0	1	1
	Philorheithrus lacustris	1	0	0
	Philorheithrus latensis	0	0	1
Polycentropodidae	*Plectrocnemia maclachlani*	1	0	0
	Polyplectropus puerillis	1	1	1
Psychomyiidae	*Zelandoptila moselyi*	0	1	0

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